LYGUS ELISUS (VAN DUZEE) AND *LYGUS BOREALIS* (KELTON) REPRODUCTION IN CANOLA AND FORAGE CROPS IN SOUTHERN ALBERTA

A Thesis

Submitted to the Faculty

of

Graduate Studies

The University of Manitoba

by

Jennifer K. Otani

In Partial Fulfilment of the

Requirements for the Degree

of

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THE UNIVERSITY OF MANITOBA

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Lygus Elisus (Van Duzee) and *Lygus Borealis* (Kelton)

Reproduction in Canola and Forage Crops in Southern Alberta

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Jennifer K. Otani

A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of Manitoba in partial fulfillment of the requirements of the degree of

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ABSTRACT

Lygus movement is associated with feeding but reproduction may affect the movement of this important pest. *Lygus* reproductive biology and host phenology may be associated with each other and may affect which hosts are invaded, when movement occurs within a season, and which individuals participate in movement.

Egg development and size of seminal depository of unmated and mated *L. elisus* females was characterized for individuals that were colony reared. In colony reared *L. elisus*, egg development occurs independent of mating. Previtellogenic, vitellogenic, then chorionated oocytes are present in 4, 5, and 7 d old unmated and mated females. Mating results in expansion of the seminal depository. Gradually, with time, the seminal depository decreases in size and the number of chorionated oocytes within ovarioles decreases. Multiple mating is suspected to occur in *L. elisus* females.

Lygus elisus and *L. borealis* sex ratios, female mating status, and egg development status were determined in individuals collected with a sweep-net from early (seeded May 11) and late (seeded June 14) stands of annual canola and perennial forage crops in 1994 and 1995. Both *L. elisus* and *L. borealis* females appeared to utilize canola for oviposition. High frequencies of females of both species were mated and ready to oviposit in canola while high frequencies of females in the forage crops, during corresponding time periods, were unmated and not reproductively mature enough to contain chorionated oocytes. The results indicate that canola and forage are utilized by

both *L. elisus* and *L. borealis* differently during the period studied and that reproductive development may affect movement.

Although male to female sex ratios fluctuated temporally in sweep-net collections performed in canola and forage crops, no pattern was apparent. Sex ratios fluctuated between male and female between sampling periods examined which suggests that both males and females participate in continuous movement in the field. Based on female mating status and egg development, high frequencies of mated *L. elisus* and *L. borealis* females containing chorionated oocytes were collected from the canola while high frequencies of unmated females containing previtellogenic, or vitellogenic staged oocytes were collected in forage crops. This suggests that *L. elisus* and *L. borealis* in the forage are younger than those in the canola, that both *Lygus* species utilize canola and forage crops differently based on the completion of reproductive activities, both species move into canola, and *L. elisus* and *L. borealis* exhibit a movement pattern in which reproductively mature individuals participate in dispersal.

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LIST OF ABBREVIATIONS

ACa, Alimentary Canal
Ch, Chorionated oocyte(s)
F1, Pro-Femur
F2, Meso-Femur
GF, Green fat bodies
ID, Internal structure within seminal depository
OA, Ovariole(s)
OP, Osteolar peritreme
OrS, Orange scent sac
Ov, Ovipositor
Pr, Previtellogenic oocyte(s)
SeD, Seminal depository
T, Tubule(s)
V, Vitellogenic oocyte(s)

1. INTRODUCTION

1.1 The problem

Lygus are highly mobile insects (Stewart and Gaylor 1994a) found in several different host species including economically valuable crops (Section Two). They feed on meristematic and reproductive host tissues and consequently inflict damage (Hori 1976) that can affect yields in valuable crops (Butts and Lamb 1990; 1991). Typically, *Lygus* movement into different hosts has been attributed to feeding, however, movement to different hosts, including into economically valuable host crops, may be an adaptation to locate mates or to find suitable oviposition sites.

Reproduction, as well as feeding, should be considered in understanding *Lygus* movement. Studying the reproductive status of *Lygus*, in relation to seasonal host phenology, may add to our understanding of the relationship between reproduction and movement. This relationship may affect which hosts are invaded, when movement occurs within a season, and which individuals participate in movement. This information has implications for management strategies aimed at controlling this important pest.

1.2 Objectives

The objective of the research described was to determine the reproductive status of *L. elisus* and *L. borealis* present in forage and canola crops in southern Alberta over the rosette, bud, and early flower development periods of canola. Specific objectives of

this study were:

(1) To characterize the reproductive development of *L. elisus* in relation to days of adult development.
(2) To describe the mating status of female *L. elisus* and *L. borealis* collected from forage and canola crops.
(3) To determine egg development status in *L. elisus* and *L. borealis* collected from forage and canola crops.

Description of *L. elisus* and *L. borealis* populations, and determination of female mating status and egg development in relation to canola crop phenology provide information about *Lygus* populations found in forage and canola crops but, more importantly, indicate how *Lygus* adults utilize both crops. Mating status and egg development data indicate which *Lygus* individuals move and may provide clues as to why they move and when this occurs. Reproductive status information has implications for *Lygus* management and might expand the understanding of *Lygus* movement.

1.3 Thesis Organization

The thesis is divided into four main sections: Introduction, Literature Review, Research , and General Discussion. The Literature Review introduces information on *Lygus* seasonal biology, host range, mirid movement, and outlines a proposed model of *Lygus* movement. The Research section describes new research examining *L. elisus* reproductive development and *L. elisus* and *L. borealis* mating and egg development in forage and canola crops. Studies addressing the three specific objectives outlined above compose the Research section. Specific objectives are examined in two sections in the

style of a scientific paper. The general discussion relates important observations from the two research papers and provides general conclusions on the reproductive status of *L. elisus* and *L. borealis* found in forage and canola crops in southern Alberta and *Lygus* movement.

2. LITERATURE REVIEW - THE FUNCTION OF *LYGUS* MOVEMENT.

2.1 Introduction

In southern Alberta, the genus *Lygus* is represented by *Lygus elisus* Van Duzee, *L. hesperus* Knight, *L. borealis* Kelton, *L. lineolaris* Palisot de Beauvois, *L. rubrosignatus* Knight, *L. shulli* Knight, and *L. solidaginis* Kelton (Kelton 1980). *Lygus* occur as a complex (Fye 1982) in the field with several coexisting species which inflict similar damage on hosts. They are capable of feeding on numerous plants of unrelated genera in different orders (Kelton 1980). Their host range includes weeds, field crops, vegetable crops, and fruit crops (Table 1).

Lygus damage a variety of economically important crops (Table 1). Both *Lygus* adults and nymphs prefer to feed on meristematic and reproductive tissues of the host plant (Spangler et al. 1993; Strong 1970). Meristematic tissue, meristems, or apical meristems are regions of the plant where undifferentiated cells are rapidly dividing to form new plant tissues. These regions are located at the tips of roots and shoots (Raven et al. 1986). Buds and developing seeds also contain meristematic tissue.

Seasonal Biology. *Lygus* overwinter as unmated adults (Ridgeway and Gyrisco 1960; Strong et al. 1970). Overwintered *Lygus* females emerge and oviposit through May, June, and July in Canada (Kelton 1983). In the early spring, overwintered adults emerge and feed. After mating, *Lygus* oviposit eggs singly but in clusters (Chittenden

Table 1: Partial *Lygus* host list adapted from the literature.

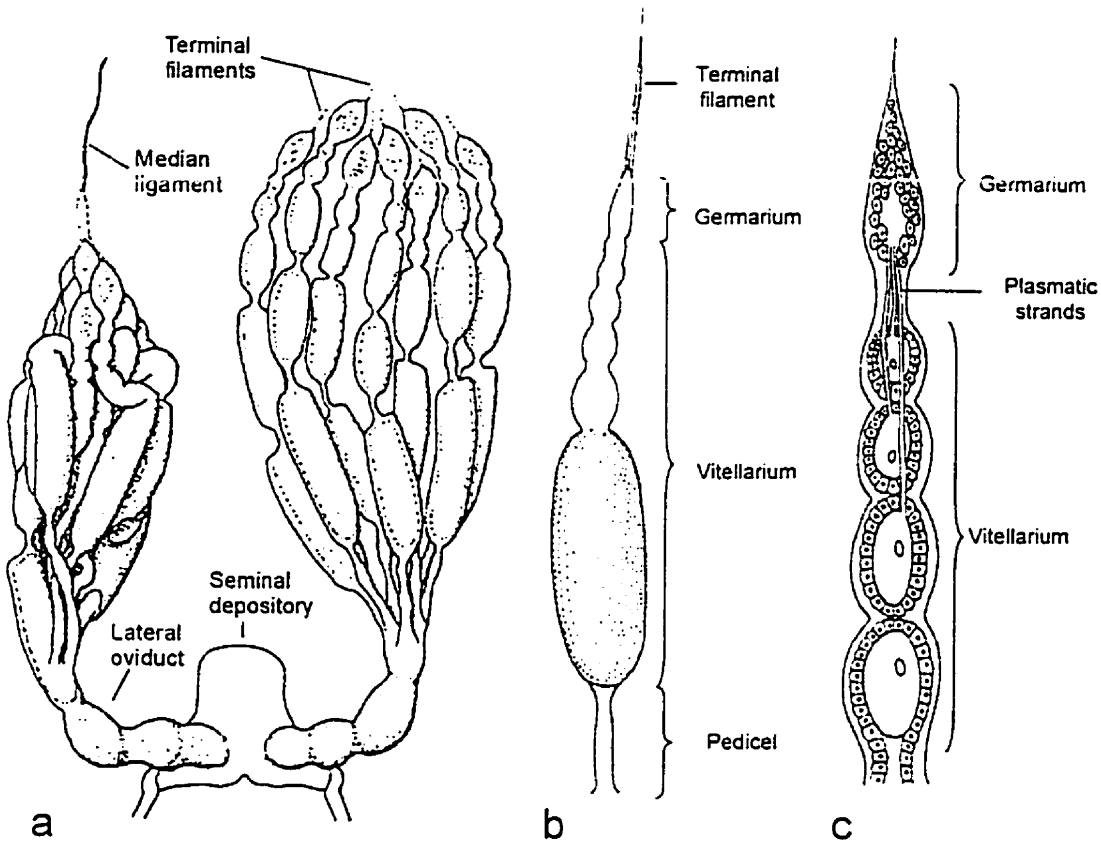
Weeds		
Prickly lettuce	*Lactuca serriola* L.	Hagel (1978)
Perennial sowthistle	*Sonchus arvensis* L.	Hagel (1978)
Canada thistle	*Cirsium arvense* (L.) Scop.	Hagel (1978)
Henbit	*Lamium amplexicaule* L.	Hagel (1978)
Narrow leaf vetch	*Vicia angustifolia* L.	Hagel (1978)
Field chickweed	*Ceratium arvense* L.	Hagel (1978)
Curly dock	*Rumex crispus* L.	Hagel (1978)
Shepardspurse	*Capsella bursa-pastoris* (L.) Medic.	Fye (1980; 1982); Schwartz and Foottit (1992)
Lambsquarters	*Chenopodium album* L.	Fye (1980; 1982); Reid et al. (1976)
Kochia	*Kochia scoparia* (L.) Schrad.	Fye (1980; 1982); Schwartz and Foottit (1992)
Redroot pigweed	*Amaranthus retroflexus* L.	Fye (1980; 1982)
Russian thistle	*Salsola iberica* L.	Fye (1980; 1982)
Flixweed	*Descurainia sophia* (L.) Webb	Fye (1980; 1982)
Goldenrod	*Solidago* spp.	Fye (1980; 1982)
Russian knapweed	*Centuarea repens* L.	Fye (1980)
Field Crops		
Cotton	*Gossypium hirsutum* L.	Cleveland (1982); Guteirrez et al. (1977); Hanny et al. (1977); Sevacherian and Stern (1975)
Alfalfa (seed)	*Medicago sativa* L.	Craig (1983); Fye (1980); Sevacherian and Stern (1974); Sorenson (1936); Soroka and Murrell (1993)
Birdsfoot trefoil	*Lotus corniculatus* L.	Schwartz and Foottit (1992); Wipfli et al. (1990)
Wheat	*Triticum* spp.	Varis (1995)
Mustard	*Brassica juncea crispifolia* L.	Stewart and Gaylor (1991)
	Sinapis alba L. and *S. arvensis* L.	Schwartz and Foottit (1992)
Canola	*Brassica napus* L.	Butts and Lamb (1990; 1991); Gerber and Wise (1995)
	Brassica rapa L.	Schwartz and Foottit (1992);Turnock et al. (1995)
Sunflowers	*Helianthus annuus* L.	Fye (1982)
Lentils	*Lens culinaris* Medik	Schotzko and O'Keeffe (1989)
Vegetable crops		
Celery	*Apium graveolens* L.	Boivin et al. (1991); Khattat and Stewart (1975)
Green beans	*Phaseolus vulgaris* L.	Khattat and Stewart (1975)
Sugarbeets	*Beta vulgaris* L.	Tamaki and Hagel (1978)
Fruit crops		
Apple	*Malus* spp.	Hauschild and Parker (1976); Kelton (1980)
Apricot	*Prunus armeniaca* L.	Kelton (1980)
Peach	*Prunus persica* L. Batsch.	Kelton (1980)
Plum	*Prunus domestica* L.	Kelton (1980)
Raspberry	*Rubus* spp.	Kelton (1980)
Blackberry	*Rubus ursinus* L.	Kelton (1980)
Currant	*Ribes* spp.	Kelton (1980)
Thimbleberry	*Rubus parviflorus* Nutt.	Kelton (1980)
Gooseberry	*Ribis* spp.	Kelton (1980)
Strawberry	*Fragaria* spp.	Kelton (1980); Zalom et al. (1993)
Chokecherry	*Prunus virginiana* L.	Kelton (1980)
Sweet cherry	*Prunus avium* L.	Kelton (1980)

and Marsh 1910). Eggs are oviposited into the surface of the leaf petioles, terminal stem tissue, stems of fruiting bodies, and fruiting bodies (Leigh 1976).

First generation nymphs appear by mid-June in alfalfa (*Medicago sativa* L.) in southern Alberta (Salt 1945) and develop through five instars (Butler and Wardecker 1971). By mid-July nymphs become first generation adults, reproduce, and produce a second generation of *Lygus* in alfalfa by early September (Salt 1945). The total number of generations in a given locality depends upon the season and climate. Salt (1945) indicated that three generations are produced in alfalfa in southern Alberta when some overwintering individuals emerge and reproduce early.

Lygus Female Reproductive Biology. Oogenesis occurs within the ovarioles of females. In *Lygus*, paired ovaries, each with seven ovarioles are present (Fig. 1 a). Each ovariole is divided into four functional sections (Fig. 1 b). At the extreme anterior end of the ovariole is the terminal filament which combines with other terminal filaments from other ovarioles to form the median ligament. The ovarioles are maintained in position by the attachment of the median ligament to the anterior phragma of the mesonotum (Davis 1955). The next section of the ovariole is the germarium within which the primordial germ cells, and follicle cells (cystocytes and trophocytes) are located. It is the germ cells which differentiate into oogonia and later form oocytes. The third section of the ovariole is the vitellarium which contains oocytes that continue to grow in number and size, both through continued cell differentiation and deposition of vitellogen, which extends the diameter and length of the vitellarium. The vitellarium is the major portion of the ovariole (Richards and Davies 1977) due to its enlarging contents. The last section of

Figure 1. The morphology and function of *Lygus* ovarioles. (a) Internal organs of reproduction in an unmated female (adapted from Davis 1955), (b) the four functional sections of an ovariole (adapted from Romoser and Stoffolano 1998), and (c) oogenesis in an acrotrophic ovariole (adapted from Romoser and Stoffolano 1998).


Terminal filaments
Median ligament
Seminal depository
Lateral oviduct
a
Terminal filament
Germarium
Vitellarium
Pedicel
b
Germarium
Plasmatic strands
Vitellarium
c

the ovariole includes the pedicel or ovariole stalk which is a short duct that connects the egg tube with the lateral oviduct.

The manner in which nutrients are supplied to oocytes alters the contents of the germarium and vitellarium. In Hemiptera, oogenesis is meriostic, more specifically acrotrophic where trophocytes remain in the germarium, anterior to oocytes. The oocytes are progressively displaced posteriorly by newer developing oocytes. Rather than alternate with oocytes, in acrotrophic oogenesis the trophocytes in the germarium provide nutrients (RNA, glycogen, lipids, sometimes extranuclear DNA) (Richards and Davies 1977) via long plasmatic strands which must elongate with the displacement of older oocytes down the ovariole (Fig. 1 c). The secretions of median cerebral neurosecretory cells, and juvenile hormone by the corpora allata, regulate in the absorption and synthesis of nutrients supplied by the trophocytes (Richards and Davies 1977).

Eventually, an oocyte does not require nutrients and the trophocytes are no longer required and degenerate (Snodgrass 1935). The epithelial cells of the vitellarium grow inwards and enclose individual oocytes to form distinct follicles. A vitelline membrane forms from the outer layer of the oocyte between the oocyte and the follicle cells. The follicle cells then produce the chorion which encases the oocyte. An endochorion forms over the vitelline membrane by a series of sections that consist of polyphenol, tanning proteins, polyphenol, oil, and again proteins. The outer exochorion is composed of layers of soft lipoprotein followed by resistant lipoprotein laid over the endochorion. In preparation for oviposition, the epithelial plug degenerates and the oocyte breaks free of the follicular epithelium formed by the follicle cells. The oocyte enters the ovariole stalk

and so moves to the lateral oviduct.

In mirids, two valvulae form the ovipositor. Normally housed within three valvifers, the toothed valvulae are held perpendicular to the abdomen and alternately move to produce a cutting action into the selected plant tissue. Muscular contractions in the lateral oviducts move oocytes into the genital chamber which also opens to the seminal depository by a broad, slit-like orifice (Davis 1955). The muscular movements associated with the cutting action of the valvulae result in the movement of oocytes from the genital chamber to the egg channel which is formed by the two valvulae (Davis 1955). Oocytes exit the egg channel and remain in the plant tissue. As oocytes are eliminated from the posterior of the ovarioles through oviposition, anterior oocytes are displaced posteriorly into position to be oviposited.

A gravid *L. lineolaris* female contains 6-16 eggs at any time during the growing season (Ridgeway and Gyrisco 1960). However the fecundity, based on laboratory rearing of *L. lineolaris* eggs from single pairings of a field collected male and female, is estimated at 239 nymphs for overwintered females and ranges between 250 and 334 nymphs for first generation female adults (Gerber 1995). The discrepancy between egg number and fecundity may be attributable to multiple mating in both males and females. Strong et al. (1970) found that *L. hesperus* males mate up to five times and females mate at least three times. *Lygus hesperus* eggs require roughly 12.2 ±0.71 days ($\bar{x}$ ± SD) to hatch at fluctuating temperatures between 10-25°C. At the same temperature, it takes 27.2 ±1.98 days to reach adult eclosion from hatch (Champlain and Butler 1967).

Movement Among Hosts. *Lygus* are strong fliers and, based on flight mill

experiments, they are capable of travelling 12 km within a 12 hour period (Stewart and Gaylor 1994a). The insects' wide host range includes species of plants which are available for *L. lineolaris* to utilize at various periods during the season (Fig. 2). An example of recorded *Lygus* incidence within a season in California demonstrates how mobility and wide host range contribute to seasonal *Lygus* movement (Stern 1976) (Fig. 3). Between April and May *Lygus* are found on weed hosts and by early May until early June they are present on alfalfa (Stern 1976). In mid-June, *Lygus* adults move from alfalfa that is cut for hay to fruiting cotton (Fig. 3) (Stern 1976). In Canada, *Lygus* immigrate to canola presumably from forage crops and nearby wild hosts which were available and utilized earlier in the season (Butts and Lamb 1990).

Lygus move between different host species and the movement from one host to another is not well understood. Understanding when *Lygus* move between host crops and which individuals participate in this type of movement may help us to reduce damage of canola by *Lygus*.

Mirid Movement Patterns. Two types of mirid flight activity are described by Waloff and Bakker (1963) in their study of five mirid species *Orthotylus adenocarpi* (Perris), *O. virescens* (Douglas and Scott), *O. concolour* (Kirschbaum), *Heterocordylus tibialis* (Hahn), and *Asciodema obsoletum* (Fieber) on a stand of broom (*Sarothamnus scoparius* (L.) Wimm.). These species of mirids are univoltine and overwinter as eggs. Their movements were classified as (1) movements within the habitat or broom stand related to mating referred to as "flitting" or (2) movements outside of the habitat referred to as "flight" (Waloff and Bakker 1963).

Figure 2. Seasonal availability of some selected plant hosts of the tarnished plant bug in the delta of the Mississippi. Adapted from Cleveland (1982).

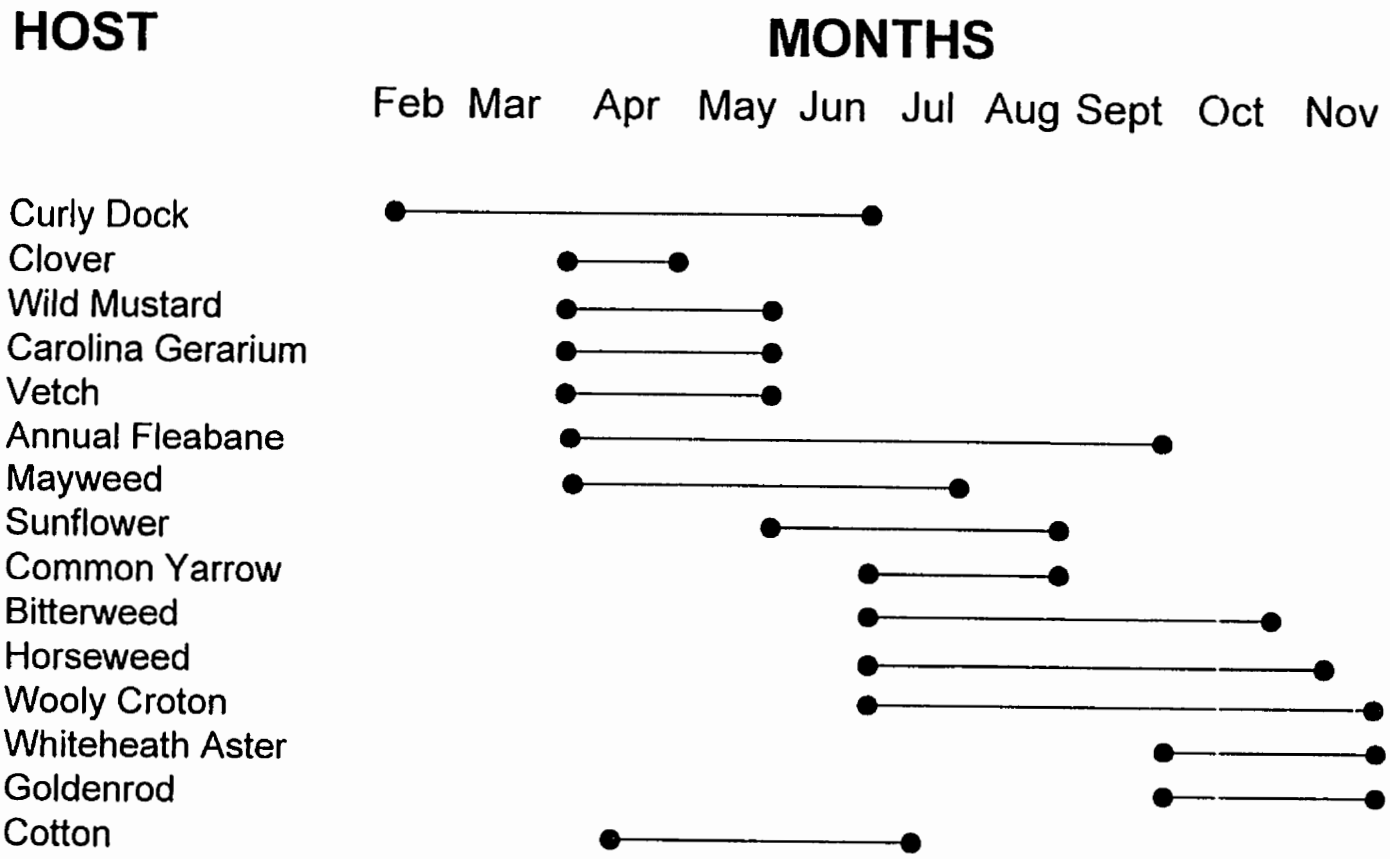
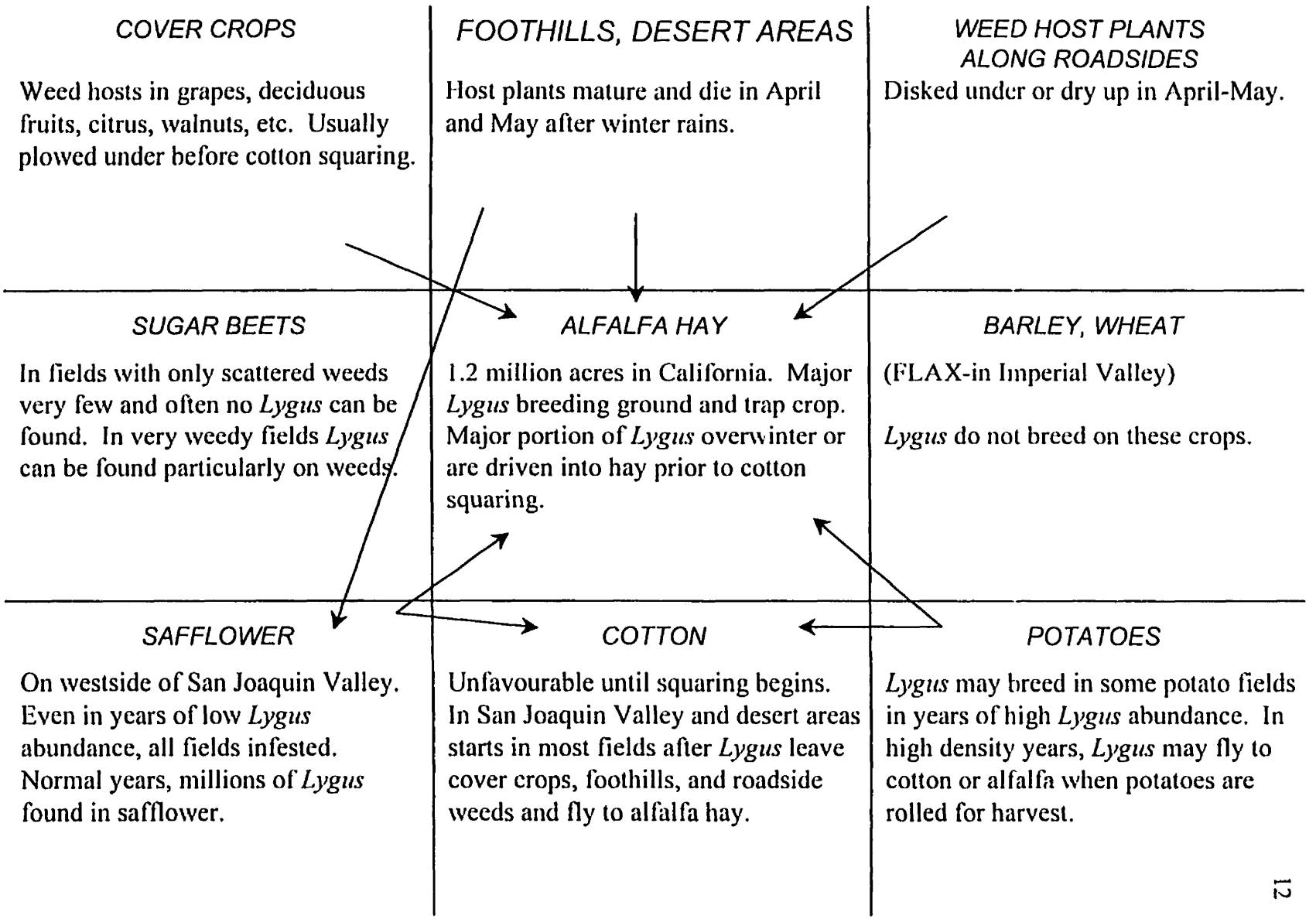

HOST
MONTHS
Feb Mar Apr May Jun Jul Aug Sept Oct Nov
Curly Dock
Clover
Wild Mustard
Carolina Gerarium
Vetch
Annual Fleabane
Mayweed
Sunflower
Common Yarrow
Bitterweed
Horseweed
Wooly Croton
Whiteheath Aster
Goldenrod
Cotton

Figure 3. Hosts and the movement of *Lygus* into alfalfa and safflower from other crops, rangelands, and weedy areas. Adapted from Stern (1976).


COVER CROPS
Weed hosts in grapes, deciduous fruits, citrus, walnuts, etc. Usually plowed under before cotton squaring.
FOOTHILLS, DESERT AREAS
Host plants mature and die in April and May after winter rains.
WEED HOST PLANTS ALONG ROADSIDES
Disked under or dry up in April-May.
SUGAR BEETS
In fields with only scattered weeds very few and often no Lygus can be found. In very weedy fields Lygus can be found particularly on weeds.
ALFALFA HAY
1.2 million acres in California. Major Lygus breeding ground and trap crop. Major portion of Lygus overwinter or are driven into hay prior to cotton squaring.
BARLEY, WHEAT
(FLAX-in Imperial Valley)
Lygus do not breed on these crops.
SAFFLOWER
On westside of San Joaquin Valley. Even in years of low Lygus abundance, all fields infested. Normal years, millions of Lygus found in safflower.
COTTON
Unfavourable until squaring begins. In San Joaquin Valley and desert areas starts in most fields after Lygus leave cover crops, foothills, and roadside weeds and fly to alfalfa hay.
POTATOES
Lygus may breed in some potato fields in years of high Lygus abundance. In high density years, Lygus may fly to cotton or alfalfa when potatoes are rolled for harvest.

Flitting is performed throughout adult life but sexually immature individuals flit for shorter periods of time (Waloff and Bakker 1963) . More males flit than females while both sexes fly equally beyond the broom habitat. A high proportion of flying females are immature. Temperatures at or below 10°C result in decreased flitting and males are more sensitive to the cold than females. The age and sex of the mirids influence which individuals take part in reproductive or dispersal movements (Waloff and Bakker 1963).

Lygus follow a crepuscular flight pattern in which a high proportion of adults fly within 2.4 m of the ground. Based on sticky trap catches, 90% of trapped *L. hesperus* and *L. elisus* fly no higher than 1.8 m from the ground and over 50% of both species are caught between 30 - 122 cm from the ground (Mueller and Stern 1973). Butler (1972) found that the majority of *L. hesperus* fly within 236 cm of the ground while Ridgeway and Gyrisco (1960) found that *L. lineolaris* fly within 0-91 cm of the ground. The height of flight exhibited by *Lygus* may be related to the height of the host crop (Mueller and Stern 1973). In the field, *L. hesperus* fly between 20:00-22:30 (Butler 1972) which is similar to *L. lineolaris* and *L. elisus* which exhibit peak levels of flight between 20:00-21:00 (Mueller and Stern 1973).

2.2 *Lygus* Movement

Lygus movement into valuable crops has the potential to cause economically important yield losses as a result of feeding activities (Butts and Lamb 1990). It is therefore useful to investigate when and why *Lygus* move from one host to another.

2.2.1 Movement in Insects

Insect movement is often classified as migration or dispersal. Kennedy's (1961) definition of migration and dispersal, based on work performed on *Aphis fabae*, defined migration as persistent, straightened-out movement permitted by the inhibition of responses such as feeding or reproduction. When feeding or reproduction are no longer inhibited, the persistent movement would be suppressed (Kennedy 1961). Dispersal was defined by Kennedy as non-migratory movement (Kennedy 1961). According to Johnson (1966), migration is influenced by an oogenesis-flight syndrome which posits that migration occurs prior to oogenesis and reproduction so that young adults move from unfavourable habitats and colonize available new habitats. Thus the oogenesis-flight syndrome proposes colonization by pre-reproductive adults as a result of increasing population pressures (Johnson 1966). Southwood (1962) suggested that migration allows a species to follow the changes occurring in the habitat. Immigration from temporary habitats occurs when the available resources are exploited and other, new habitats become available (Southwood, 1962). Southwood (1962) also concluded that these migratory events would be stimulated by proximate stimuli (eg. photoperiod, crowding, or changes in host plant physiology). Another concept in insect migration follows Johnson (1966) in that it favours migration of individuals which have a high rate of population increase (Dingle 1972). Dingle (1982) proposed that migrating individuals should move to habitats suiting the development of offspring. In order to achieve this adaptive type of dispersal, the migrating individuals should move prior to reproductive maturity, and possess a high reproductive value meaning individuals would contribute greatly to

population growth upon arrival (Dingle 1972).

2.2.2. The Function of Adult Dispersal in *Lygus* Life History

Food quality, food quantity and population density are interrelated and often jointly studied for their effect on insect movement. These three ecological factors influence flight capability and movement in some Heteroptera. Lack of food stimulates flight and defers ovarian development and flight muscle histolysis in *Dysdercus* spp. (Heteroptera), which are facultative migrants (Dingle and Arora 1973). Density does not affect the proportions of mirid species moving away from broom (Waloff and Bakker 1963). Mueller and Stern (1973) found that the population density of *L. elisus* remained relatively constant through the season with relatively equal numbers entering and leaving safflower fields monitored with two-sided sticky traps. More *L. hesperus* entered than left in the same monitored fields. However, *L. elisus* which were at lower densities than *L. hesperus* were more prone to flight activity.

Ecological and behavioural theories exist which attempt to predict when and why migration or dispersal occurs in insects. However, controversy surrounds the definition of 'insect migration' (Rankin and Singer 1984) and the subject of 'insect dispersal' (Johnson 1966). Rankin and Singer (1984) avoided use of the term insect migration and chose to review insect movement which encompasses short-distance foraging and long-distance migration. In the manner of Rankin and Singer (1984), the following is a review of some of the factors associated with insect movement and how it may apply to when and why *Lygus* move from one host to another.

Host Preference. If adult *Lygus* move to find feeding sites, and they exhibit feeding preferences, a relationship between the availability of preferred food and movement to that food is likely to be evident. *Lygus* show a preference for meristematic and reproductive plant tissues (Spangler et al. 1993; Strong 1970). Therefore, if *Lygus* movement is the result of finding feeding sites, movement to host sites, presence and damage by *Lygus*, and movement from hosts lacking preferred food items should occur.

The seasonal host plant sequence for *L. lineolaris* in the California Delta was recorded (Fig. 3). The hosts plants examined in Figure 3 include drying weeds and potatoes at harvest stage. *Lygus lineolaris* move from the weeds and potatoes lacking meristematic or reproductive tissues to alfalfa which produces meristematic or reproductive tissues for long periods in the growing season or presquaring cotton (Fig.2). *Lygus lineolaris* is present on tender plants plus other early weeds in late winter and early spring in the Mississippi Delta (Cleveland 1982). *Lygus* are found in alfalfa during the early vegetative stage, flowering and seeding periods (Fye 1982). *Lygus* move into beans until the crop matures (Hagel 1978). Spangler et al. (1993) found that *L. lineolaris* adults are strongly attracted to ripe fruit and may be present in bramble plantings during fruit-ripening. *Lygus hesperus* and *L. elisus* move from hosts plants beginning to dry due to water stress (Sevacherian and Stern 1974) and almost all *L. hesperus* move to another field when alfalfa is cut (Butler 1972). Based on these observations, it would seem that *Lygus* perceive host quality and move to or depart from hosts based on the availability of meristematic and reproductive tissues. *Lygus* movement appears to be related to the need to procure food and the location of preferred food items.

Lygus population peaks occur at periods of production of meristematic and reproductive plant tissues. Adult *L. lineolaris* populations increase in soybean fields during the full bloom and peak at the pod set stage (Poston and Pedigo 1975). In southern Manitoba, adult *L. lineolaris* are found in canola from the rosette to pod stages of development (Leferink and Gerber 1997). Adult *L. lineolaris* populations peak in canola during bud (Gerber and Wise 1995), flowering (Gerber and Wise 1995; Leferink and Gerber 1997; Timlick et al. 1993), and again at the pod stage in southern Manitoba (Timlick et al. 1993). Recorded peaks of *L. lineolaris* adult and nymph abundance in brambles (raspberry and blackberry) occur at the bloom to green fruit stages and fruit-ripening stages in central New York (Spangler et al. 1993). High populations of adult *L. lineolaris* coincide with trefoil blossom setting between late June and early July in Wisconsin (Wipfli et al. 1990). Therefore, *Lygus* population peaks which can indicate movement, are associated with the seasonal availability of meristematic or reproductive plant tissues for various host plants.

Insect damage, although dependent of plant response, can also indicate insect presence. By comparing when *Lygus* damage is occurring in hosts in relation to host development stage one can infer what plant stage is utilized or even preferred by the insect and when the insect moves into the host. Heavy damage occurs in cotton during the stages of presquaring (Hanny et al. 1977), squaring (Gutierrez et al. 1977), and up to boll setting (Cleveland 1982) indicating a synchronous presence of the insect with the production and availability of cotton meristematic and reproductive tissue. Young sugarbeet seedlings require protection from *L. hesperus* and *L. elisus* (Tamaki and Hagel

1978). *Lygus lineolaris* will damage green beans at the flower and pod setting stages (Khattat and Stewart 1975). Feeding causes abscission of buds and flowers, collapse of seeds, and a reduction in weight of healthy seeds in *Brassica rapa* (Butts and Lamb 1990). To control *Lygus* damage in *B. napus* and *B. rapa*, recommended insecticidal applications are applied at the early pod stage as this coincides with the peak *Lygus* population in northern Alberta (Butts and Lamb 1991). From these results, it is evident that there is a strong relationship between the presence of *Lygus* and the abundant availability of preferred meristematic and reproductive tissues.

Reproduction. Many insects move in response to their reproductive biology. Reproductive processes may be associated with when and why *Lygus* move because host choice and host utilization may be the result of these processes.

Heterosexual and hermaphroditic individuals, because of their mode of reproduction, are required to locate mates to reproduce and this usually involves movement of one individual to find a compatible, sexually receptive conspecific. Mate location is strongly affected by whether females mate once or mate multiple times (Thornhill and Alcock 1983). In monogamous species, males search early for young females (Thornhill and Alcock 1983). An example of this is the solitary bee (*Centris pallida* Fox) which mates only once. Newly eclosed, virgin females are sought out at a particular time of the season by adult males which emerge before females.

Insect species which mate multiple times increase the number of opportunities available for adults to mate and a multiple mating system alters the time when males are seeking mates. When females mate multiple times, males are more prone to search for

females just prior to oviposition (Thornhill and Alcock 1983). *Lygus hesperus* females mate and oviposit multiple times (Strong et al. 1970). In laboratory studies *L. hesperus* males mate up to five times within a 5 day period (Strong et al. 1970). Female *L. hesperus* mate up to three times within a 13 day period (Strong et al. 1970). Based on *L. hesperus*, multiple mating opportunities are likely present for all *Lygus* species and this might affect when and where males and females seek mates.

Mating behaviour dictates how and where insects move in order to interact with mates. *Lygus* mate while in contact with a substrate thus mating might occur on some part of a host plant. Evidence from the laboratory indicates that either a male or female *L. lineolaris* is able to initiate copulation using visual cues (Strong et al. 1970) and proximity may affect communication. When a pair of adult *L. lineolaris* are placed in a cage (interior diameter 2.5 cm x height 2.5 cm) the two individuals become quiet, remaining immobile (Strong et al. 1970). Both individuals begin a slow walk and when both antennae of the male contact the female, the male begins an aggressive behavioural pattern consisting of vertical jerking and quivering of its abdomen (Strong et al. 1970). When the male approaches from the right side of the female, he places his abdomen under the right side of the female and attempts to copulate with the tip of his abdomen toward the base of the female's ovipositor (Strong et al. 1970). A receptive female bends her ovipositor 180° to allow the tip to extend posteriorly (Strong et al. 1970). In some situations a female initiates copulation, signals receptiveness by bracing her legs and raising her abdomen or even approaching the male then tapping her abdomen on the substrate causing an audible noise (Strong et al. 1970). This behaviour by the female

results in the male initiating his aggressive behaviour previously described and copulation follows (Strong et al. 1970).

Lygus movement is affected by the reproductive development of the adult. Age, sex, and egg development influence which *Lygus* move and the pattern of their movement from one host to another. Typically younger adults and parous female *L. lineolaris* individuals colonize a host patch of preflowering mustard (*Brassica juncea crispifolia*) (Stewart and Gaylor 1991). Gerber and Wise (1995) suggest first-generation females disperse from host alfalfa and strawberries when the females become reproductively mature. Stewart and Gaylor (1994a) examined the flight activity of laboratory reared (27°C) *L. lineolaris* using a flight mill and concluded that reproductive females are most inclined to colonize. Stewart and Gaylor (1994a) found that females with chorionated eggs flew seven times longer than egg-less female *L. lineolaris*. Reproductive males and females had longer cumulative flights than other age classes of adults and females flew longer than males in cumulative flights (Stewart and Gaylor 1994a). Reproductive maturity, determined by age and associated with the development of eggs, predisposes individuals to fly for longer periods, and yet, Stewart and Gaylor (1994a) found that pre-reproductive females fly farther on single flights than do reproductive females. Reproductively mature *L. lineolaris*, indicated by the older age and the presence of chorionated oocytes, are more prone to ly longer using numerous, short distance flights. Pre-reproductive *L. lineolaris* make fewer, longer distance flights. Females, pooled over all age classes, have a longer cumulative flight period (211.4 ± 34.7 min) than males (34.2 ± 13.4 min) during a 12 hour period (Stewart and Gaylor 1994a). In addition,

females with chorionated eggs exhibit almost seven times longer cumulative flight durations than egg-less females while the age of the female does not affect the duration of the cumulative flight (Stewart and Gaylor 1994a).

Location of mates and the movement pattern associated with it may be affected by the use of pheromones. *Lygus* may use pheromones in mating and affect the pattern of movement conspecifics use to locate and mate with each other. There is evidence that pheromones are used in *Lygus* mating. Graham (1987; 1988), Scales (1968), and Strong et al. (1970) observed movement of individuals and males to traps baited with conspecifics and females, respectively. However, the only isolated and synthesized pheromone found for a mirid is that of the mullein bug (*Cammylomma verbasci* Meyer) (Smith et al. 1991) and no pheromones has been isolated for *Lygus* to date. Until a pheromone is isolated, the full effect of pheromones in mating and their effect on mate location remain unknown.

Insect-Plant Interactions and *Lygus* Movement. Polyphagous, highly mobile insects like *Lygus* have several potential hosts available to exploit in the season. Fye (1980) recorded *Lygus* on kochia (*Kochia scoparia* (L.) Schrad.), ragweed (*Ambrozia artemisiifolia* L.), horseweed (*Conyza canadensis* (L.) Cronq.), marsh-elder (*Iva xanthifolia* Nutt.), and goldenrod (*Solidago* spp.) during early August to October in eastern Washington. The condition of these host plants plays a role in the movement between hosts. *Lygus hesperus* and *L. elisus* move from dry or water stressed alfalfa (Sevacherian and Stern 1974) and mature fleabane (*Erigeron strigosus*) (Stewart and Gaylor 1994b). The fecundity of *Lygus* is also affected by host selection. In a

comparison of fleabane and cotton (*Gossypium hirsutum* L.), a higher number of *L. lineolaris* eggs were oviposited on fleabane (Stewart and Gaylor 1994b). In addition to low numbers of eggs being oviposited on cotton, subsequent *L. lineolaris* nymphal survivorship on this host is low (Fleischer and Gaylor 1988). *Lygus lineolaris* oviposition choice experiments using celery, carrot, and beans show that the insects may choose to oviposit on hosts which are inimical to egg and nymph development (Curtis and McCoy 1964). Gerber (1997) found that there is no difference in the resulting number of *L. lineolaris* nymphs emerging from eggs when two *Sinapis* and four *Brassica* species were available for oviposition. However, *L. lineolaris* adults are more abundant on *B. juncea* (L.) Czern than on *B. napus* L., *B. carinata* Braun, *S. alba* L., and *S. arvensis* L. (Gerber 1997). Therefore although *Lygus* have many hosts to choose from and movement occurs when the host plant deteriorates, the hosts preferred for oviposition may not be the best host for nymphal survival and development.

2.3 Discussion

Much work has been done in the areas of insect migration and dispersal (Dingle 1972; Johnson 1966; Kennedy 1961). While some ecological and biological factors may influence *Lygus* movement, no model exists which helps one understand how *Lygus* move into economically important fruit, vegetable and cereal crops. In this discussion a possible model is suggested.

Reproductive processes may be involved in the pattern of *Lygus* movement, *Lygus* host selection, and host crop utilization. Movement after feeding is associated with

seasonal decline of host quality but *Lygus* reproductive processes (eg. mate location, copulation, or oviposition) may also be associated with *Lygus* movement. The completion of reproductive processes may even supersede host selection on the basis of feeding. A plant host suitable for feeding may be unsuitable for reproduction, therefore, reproductive adults may be required to move to find a suitable host to complete reproduction. Thus, one would expect that *Lygus* movement and host utilization follows a different pattern in pre-reproductive and reproductive adults.

Herbivorous insects are linked to the biology of their host or hosts. Monophagous insects, by definition, feed on one species of plant (Jolivet 1992) and are therefore restricted to that plant species' distribution and biology. Even though several host individuals may be present, a limited window of opportunity, defined by the host biology, determines when the monophagous insect can exploit its host. In contrast, polyphagous, multivoltine *Lygus* have been shown to move sequentially within and between generations, to various host plant species (Fye 1980). The timing of *Lygus* presence, population peaks, and damage in several host crops indicates a strong preference for periods of abundant meristematic tissue production. Th asynchronous production of abundant meristematic tissue or reproductive tissues by several plant species throughout the season is linked to the sequential movement between hosts by *Lygus*. Stern's (1976) example of *Lygus* movement in California in an agricultural habitat demonstrates that the availability of meristematic tissue and reproductive plant tissue permits *Lygus* to move to or from a particular plant host (Fig. 3). *Lygus* move into a crop that provides abundant production of meristematic and reproductive tissues and emigrates from alfalfa producing

few buds and flowers. *Lygus* move into cotton which, at that time in the season, produces buds and flowers, the preferred feeding tissues. Fye (1980) found that the major species of weeds in eastern Washington form a perfectly sequenced host range of species for *Lygus* throughout the season beginning with early crucifers, chenopods in mid-season to fall, then composites in the late season.

Feeding and the location of feeding sites is associated with movement. If a preference is exhibited in the feeding behaviour of the insect, some relationship should be evident between the availability of the preferred item and movement of the insect towards that preferred item. The synchronous appearance of *Lygus* population peaks and plant host production of the meristematic and reproductive tissues indicate that *Lygus* movement is mediated by the search for food. This is emphasized by the timing of damage by *Lygus* in crops and the recorded plant sequences for *Lygus* species.

Feeding and thus feeding preferences may determine when and why *Lygus* move. However, the insect's reproductive biology may control which adults fly to a new areas and which individuals move from one host to another within the same area. Longer single flights may be permitted because the pre-reproductive females do not participate in mating and oviposition activities which demand close contact with the host where mates and oviposition sites are located.

Lygus mate multiple times with oviposition occurring between matings. Eggs are laid singly, but in clusters, however *Lygus* females do not oviposit all their available eggs in one location. Comparison of the oviposition pattern (Chittendon and Marsh 1910) and the reported fecundity (Gerber 1995) indicate that *Lygus* females oviposit a few eggs on

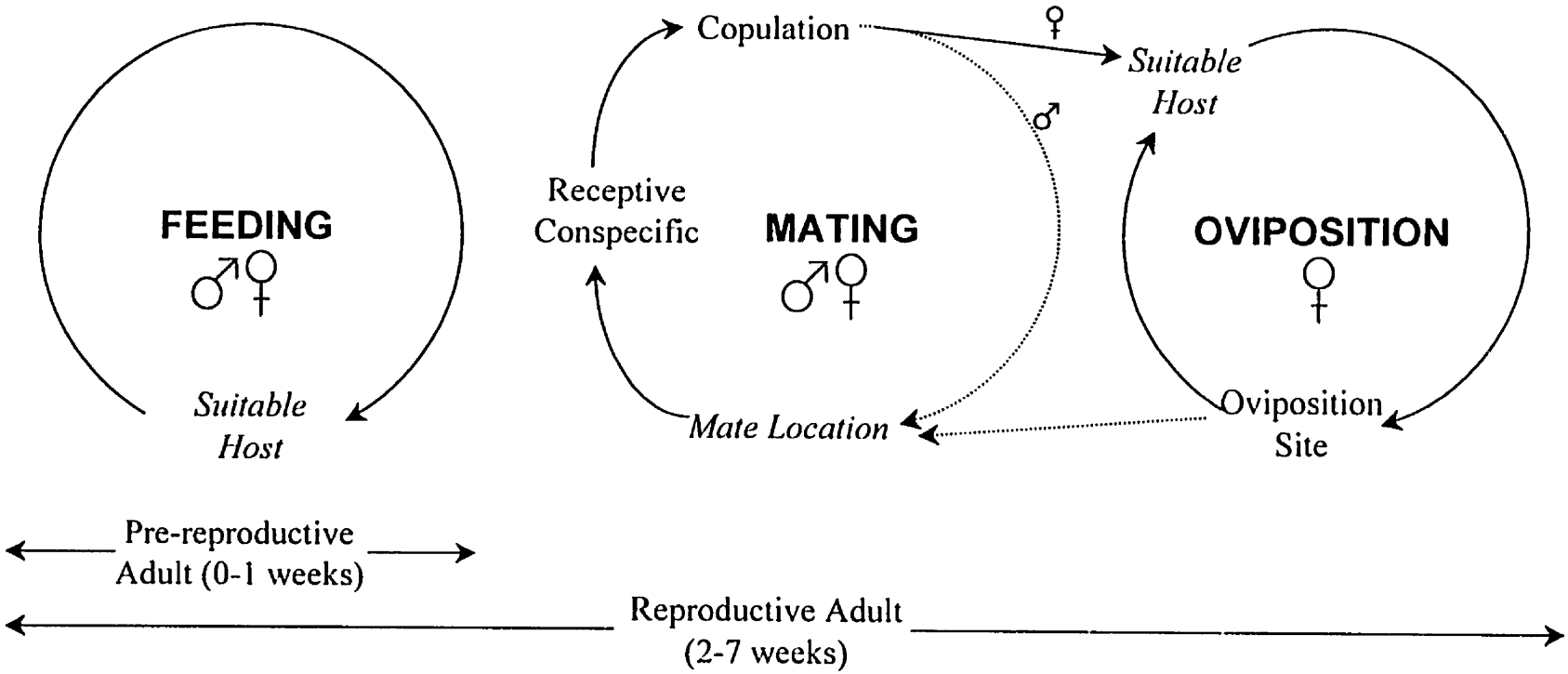
an appropriate host then move to another site to continue oviposition. Therefore, reproductive females are prone to make several, short flights or flit (Waloff and Bakker 1963). The fact that parous females are predisposed to fly longer than egg-less female *L. lineolaris* suggests that a reproductive female searches for oviposition sites to void herself of eggs and continues to move until her full complement of eggs are oviposited.

Proposed Model of *Lygus* Movement. One hypothesis for *Lygus* movement is that a hierarchy of basic biological events are associated with movement in *Lygus*, with age and sex influencing the patterns of movement (Fig. 4). The location of feeding sites and host plant phenologies provide the range of hosts available and movement will occur between these, but the age and sex of a *Lygus* ultimately determines the pattern and amount of movement within the host range.

In pre-reproductive adults, feeding and the location of suitable feeding sites affect movement. Feeding is limited by the availability of preferred food items (Fig. 4, Feeding circle) and movement continues until suitable supplies of meristematic and reproductive plant tissues are located. Feeding follows location of a suitable host. If, upon alighting or following feeding, the host is unsuitable, a pre-reproductive adult moves until a suitable host is located. Host quality controls the amount and distance required to move to satisfy feeding requirements. Pre-reproductive adults are not receptive to mating until a precopulatory period of roughly 7 days has elapsed, and therefore, feeding and the location of feeding sites will govern movement until this developmental stage ends.

As the precopulatory period ends, the need to complete reproduction takes over as the main factor requiring movement by reproductives (Fig. 4, Mating and Oviposition

Figure 4. A graphic model of the biological activities associated with *Lygus* movement. Bold, solid lines (▬▬) indicate where movement to fulfill feeding, mating, or oviposition occurs. Dotted lines (▪▪▪▪▪) indicate influence of age, and italics (***Italics***) indicate where density may affect movement.


FEEDING
Suitable Host
Copulation
Receptive Conspecific
MATING
Mate Location
Suitable Host
OVIPOSITION
Oviposition Site
Pre-reproductive Adult (0-1 weeks)
Reproductive Adult (2-7 weeks)

circles). The process of mating increases movement among and between hosts. The location of feeding sites, mates, and oviposition sites will determine movement of a reproductive female. Location of feeding sites and receptive females will determine movement of a reproductive male. Although the location of suitable feeding sites and the process of feeding will dictate where reproductive adults move, mating and the location of oviposition sites should supersede finding suitable feeding sites and the pattern of movement is altered to complete reproductive processes.

To complete mating, individuals must locate suitable, receptive mates and copulation must occur (Fig. 4, Mating circle). The location of a receptive conspecific involves movement. When either no conspecifics or non-receptive conspecifics are encountered, the insect will move to find a receptive conspecific. Pheromones may mediate mate location but visual communication is also important in mate location and copulation. Within a 10.5 cm distance, *Lygus* use visual cues to communicate (Graham 1988). Based on laboratory studies, the plant surface is the medium on which *Lygus* male and female visual and tactile communication occurs.

In order to feed and participate in mating, a reproductive female will move but once the female has copulated, the process of oviposition may require further movement. A reproductive female oviposits into leaf petioles, terminal stem tissues, stems of fruiting bodies and even fruiting bodies of a host (Leigh 1976). Assuming *Lygus* have preferred plant structures for oviposition, movement by females is necessary to complete oviposition and movement should increase among and between hosts (Fig. 4, Oviposition circle). An ovipositing female needs to find several suitable areas of host tissues

resulting in increased movement among and between host plants. This movement is limited by plant structures and surface available to oviposit eggs. Finally, because the female is capable of mating multiple times, producing new eggs to oviposit with each copulation, the movement necessary to complete oviposition as an adult female is again increased.

Assuming all *Lygus* species participate in multiple mating, the oviposition period of the female will be extended until all possible chorionated oocytes are oviposited or until she dies. The movement required to find suitable oviposition sites, interrupted by locating and mating necessary to supply fertilized oocytes for oviposition will increase (Fig. 4, Mating and Oviposition circles, dotted lines). As a result of the process of mating and oviposition, a high number of short flights among and between host plants might be expected to occur which resembles Waloff and Bakker's (1983) flight versus flit movement pattern.

3. CHARACTERIZATION OF THE DEVELOPMENT OF FEMALE *LYGUS ELISUS* (VAN DUZEE) (HETEROPTERA: MIRIDAE) REPRODUCTIVE SYSTEM.

3.1 Abstract

The progression of oogenesis and the relative size of the seminal depository of unmated and mated female *L. elisus* from a laboratory-reared colony were observed and recorded using camera lucida drawings and photographic slides. Three types of oocytes, previtellogenic, vitellogenic, and chorionated, occurred within the ovarioles. Variable numbers and stages of oocytes occurred in females of different ages. Previtellogenic oocytes were present in 4-day-old females, vitellogenic oocytes in 5-day-old females, and chorionated oocytes in 7-day-old females. Egg development occurred independently of mating. Mating resulted in expansion of the seminal depository. The contents of the seminal depository slowly diminished over time suggesting that sperm and associated male donated fluids were being used to fertilize chorionated oocytes immediately prior to oviposition. The number of oocytes visible in dissections of unmated and mated females, compared to available fecundity data (Gerber 1995) suggests that *L. elisus* females mate multiple times either developing a series of batches of eggs between mating or, following a virgin mating, continues to develop eggs with later matings occurring during an extended oviposition period.

Based on the above observations, age categories were created using the size of the

seminal depository and the number of chorionated oocytes in ovarioles. The age categories were then applied to *L. elisus* and *L. borealis* females collected from canola (*Brassica napus* L. cv. Westar) and sainfoin (*Onobrychis viciaefolia* Scop. cv. Nova), to determine if the age categories were applicable and could be used to estimate the age of *Lygus* from the field. Females in the field showed the same developmental processes except that no females had fewer than 4 chorionated oocytes. Females without chorionated eggs were never mated and nearly all females with chorionated eggs were mated, implying mating occurs after females develop chorionated oocytes.

3.2 Introduction

Lygus are pests in several crops (Section Two). Most research in *Lygus* describes feeding damage, population distributions, sampling, and control methods in various important crops (Boivin et al. 1991; Butts and Lamb 1990; Chiba et al. 1978; DeBolt 1989; Fleischer and Gaylor 1988; Godfrey and Leigh 1994; Hori 1976; Schwartz and Footitt 1992; Sevacherian and Stern 1972; Wise and Lamb 1998). Very few studies of the biology of *Lygus* exist even though this genus includes some important pests of economically valuable crops. Understanding *Lygus* biology broadens the understanding of how, when, and why these insects move into and damage crops. Detailed information on the reproductive biology can improve our understanding of host utilization and *Lygus* population dynamics so that control methods might be improved.

Davis (1955) studied the morphology of mirids and also described the reproductive system of *L. lineolaris*. Oogenesis takes place in the ovarioles of the *Lygus*

female (Section 2.1). Previtellogenic, vitellogenic, and chorionated oocytes are organized anterior to posterior, respectively, within each ovariole. A right and left set of seven ovarioles are held in place by ligaments located at the anterior end of the ovarioles. The seven ovarioles converge posteriorly to form the lateral oviduct. The right and left lateral oviducts empty into the genital chamber via what is referred to as the common oviduct (Davis 1955). The genital chamber, which also opens to the seminal depository, routes oocytes to the ovipositor which deposits them into plant tissue. The seminal depository and its function as a receptacle for sperm were described by Davis (1955).

Strong et al. (1970) studied the reproductive biology of *L. hesperus* and described the mating behaviours, precopulatory period, and multiple mating habit. The reproductive system of male and female *L. hesperus* and the inflation of both the female seminal depository and genital pouch at mating were described. Strong et al. (1970) also reported possible pheromone mediated attraction of *L. hesperus* males to virgin females. Graham (1987; 1988) reported the attraction of *Lygus* species to conspecifics, although, to date, no pheromone has been isolated for any *Lygus* species.

The object of this study was to characterize the reproductive development of female *L. elisus* in relation to age. Characteristic stages of oogenesis within the ovarioles and the changes in the seminal depository were described for unmated and mated colony reared *L. elisus* females of various ages. Characterization of the progression of oogenesis and changes in the size of the sperm receptacle organ were outlined. Finally, the reproductive status of laboratory-reared females with respect to age was compared with *L. elisus* and *L. borealis* females collected from natural field populations in canola (*Brassica*

napus L. cv. Westar) and sainfoin (*Onobrychis viciaefolia* Scop. cv. Nova).

3.3 Materials and Methods

3.3.1 Characterization of Female *Lygus elisus* Reproductive Status

Rearing. A colony of *L. elisus*, established in 1994, was reared at 20-21 °C, 40-60% R.H., under a 16:8 (L:D) h cycle. The colony was divided into adult and egg rearing containers. Adults were reared in (length 30.5 cm x width 30.5 cm x height 41 cm) plexiglass cages. Three host plants were placed in each cage for feeding and oviposition. The plants were lambsquarters (*Chenopodium album* L.) and canola (*B. napus* L. cv. Westar). Plants potted in a 12.7 cm diameter pot with Cornell media were introduced into the adult cage during the bud to early flower stages of development. In 1994, two lambsquarters plants and one canola plant were added weekly to the cage. In 1995 and 1996, three lambsquarters plants were used per cage. The potted plants were supplemented with broccoli (*B. oleracea* L.) florets added to the cage every 2 days. Each month, approximately 15 poached fifth- to seventh-instar *Euxoa* spp. larvae were added to the cage. Between 50-300 adult *L. elisus* were housed in a single cage.

Each week, the potted plants were removed from the cage and exchanged for new plants. The removed plants were placed individually into a white plastic egg rearing bucket (24.5 cm dia. x 30 cm), covered with a gauze lid, and watered as required. Rearing buckets were subjected to the same temperature, humidity, and light regimen as the adult cages. Beginning seven days after plants were transferred to rearing buckets, broccoli florets were added every second day to provide newly emerged nymphs with

food. First instar nymphs emerged 9-14 days after the host plants were isolated in rearing buckets and fifth-instars were present approximately 14-28 days after egg hatching.

Female fifth-instar nymphs were isolated and reared in small, white plastic containers (12 cm dia. x 7.5 cm) with screened lids (1 mm gauge). Isolated nymphs were provided daily with broccoli florets and provided weekly with boiled *Euxoa* spp. larvae. The day of adult eclosion was recorded as day one of adult development.

Unmated Females. Females at day one of adult development were placed with other females of the same development stage in an isolation container made of white plastic (12 cm dia. x 7.5 cm) with a screened lid (2 mm gauge). Broccoli was added daily to the container and females were reared until a predetermined day of development on which individual females were removed for dissection.

Mated Females. Females were placed in an isolation container, as described above, with other females of the same development stage. Reproductively mature males (7-14 days old) were added to containers holding virgin, adult females once females were 6-7 days old. Males and females remained housed together until females were removed for dissection. Regardless of the number of females in the container, twice the number of males were added to increase the probability that mating occurred. Mating was restricted to females 6-7 days old because the pre-reproductive period of *L. hesperus* begins 7 days after adult eclosion (Strong et al. 1970).

Dissections. All dissections were performed on a binocular dissecting microscope. A female specimen was transferred from an isolation container to a plastic petri dish (45 mm dia.), then placed for 1 hour at -5 ^{0}C. The frozen specimen was

positioned on a dissection dish with the ventral side exposed at room temperature. The female was decapitated and then submerged in a physiological saline solution (0.9%). The cuticle adjacent to the anterior end of the ovipositor was separated posteriorly, exposing the posterior end of the coelom. A medial incision was made from the anterior end of the ovipositor to the posterior of the metathorax and the cuticle was then pinned laterally to expose the anterior end of the coelom. To classify the reproductive development of unmated and mated females, both the seminal depository size and egg development were used. The mating status of a female was characterized by the relative size of the seminal depository, as uninflated, inflated, partly deflated, or deflated as follows:

(1) Uninflated - the seminal depository is an uninflated, translucent, small membranous sac (0-10% of the size of an inflated seminal depository).
(2) Inflated - the seminal depository is an expanded, opaque, bulbous, greatly enlarged membranous sac.
(3) Partly Deflated - the seminal depository is an inflated, opaque, bulbous, large membranous sac (50-80% of the size of an inflated seminal depository).
(4) Deflated - the seminal depository is an uninflated, translucent, flattened, large membranous sac (10-30% of the size of an inflated seminal depository).

The stage of egg development was determined by examining the relative size of the ovarioles and the type of oocytes present within the ovarioles following Gerber and Wise (1995). *Lygus elisus* egg development was separated into three distinguishable categories from dissected, colony reared individuals based on the oocyte development observed within the transparent ovarioles and the size of the ovarioles. Females were

characterized as containing previtellogenic, vitellogenic, or chorionated oocytes.

(1) Non-reproductive - Right and left sets of ovarioles are reduced in diameter and length and transparent. Assumed to be either a newly eclosed or non-reproductive female.

(2) Previtellogenic - In both the right and left sets of ovarioles, oocytes are located in the extreme anterior ends of the transparent ovarioles. Oocytes appear as white masses rather than distinct units when present within the ovarioles. The ovarioles are reduced in diameter except at the anterior ends where the previtellogenic oocytes are housed (Fig. 5).

(3) Vitellogenic - Oocytes with yolk occupy the length of the ovarioles. These oocytes are white and visible individually within the ovarioles which are distended to contain the large sized oocytes (Fig. 6).

(4) Chorionated - Shiny, white oocytes are located posterior to vitellogenic oocytes in the ovarioles and in the common lateral oviducts. Chorionated oocytes are white and shiny and visible individually within the distended ovarioles. Chorionated tanned caps of the oocytes are discernable through the ovarioles (Fig. 7).

(5) Post-oviposition al - Small, white aggregations are visible in the extreme anterior ends of the distended, transparent ovarioles. No other oocytes are visible within the ovarioles. Suspected as oldest reproductively developed female.

Camera lucida drawings and photographic slides were made to accompany observations made from the dissected females.

Figure 5. *Lygus elisus* (Van Duzee) female with previtellogenic oocytes within her ovarioles (unmated 4-d-old).
Abbreviations: ACa, Alimentary canal; GF, Green fat bodies; OA, Ovariole(s); Pr, Previtellogenic oocyte(s); SeD, Seminal depository.

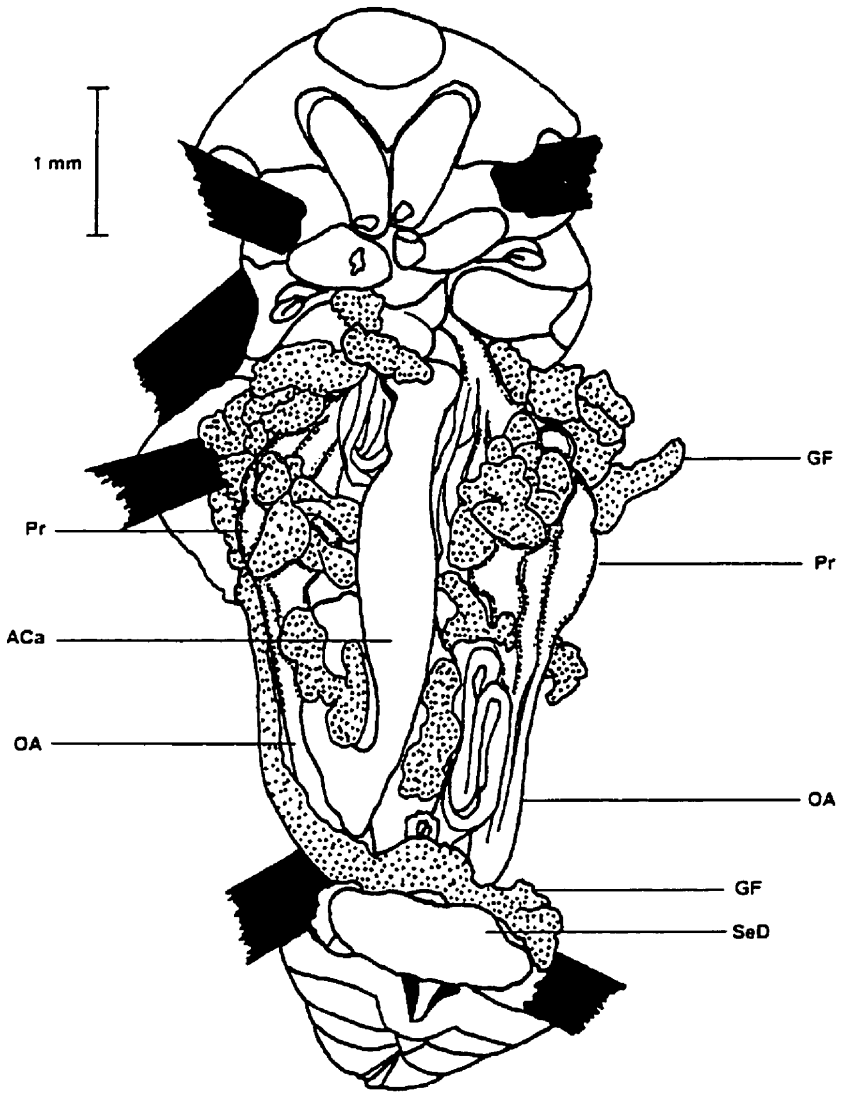

1 mm
GF
Pr
Pr
ACa
OA
OA
GF
SeD

Figure 6. *Lygus elisus* (Van Duzee) female with vitellogenic oocytes within her ovarioles (unmated 5-d-old).
Abbreviations: ACa, Alimentary canal; GF, Green fat bodies; OA. Ovariole(s); SeD, Seminal depository; V, Vitellogenic oocyte(s).

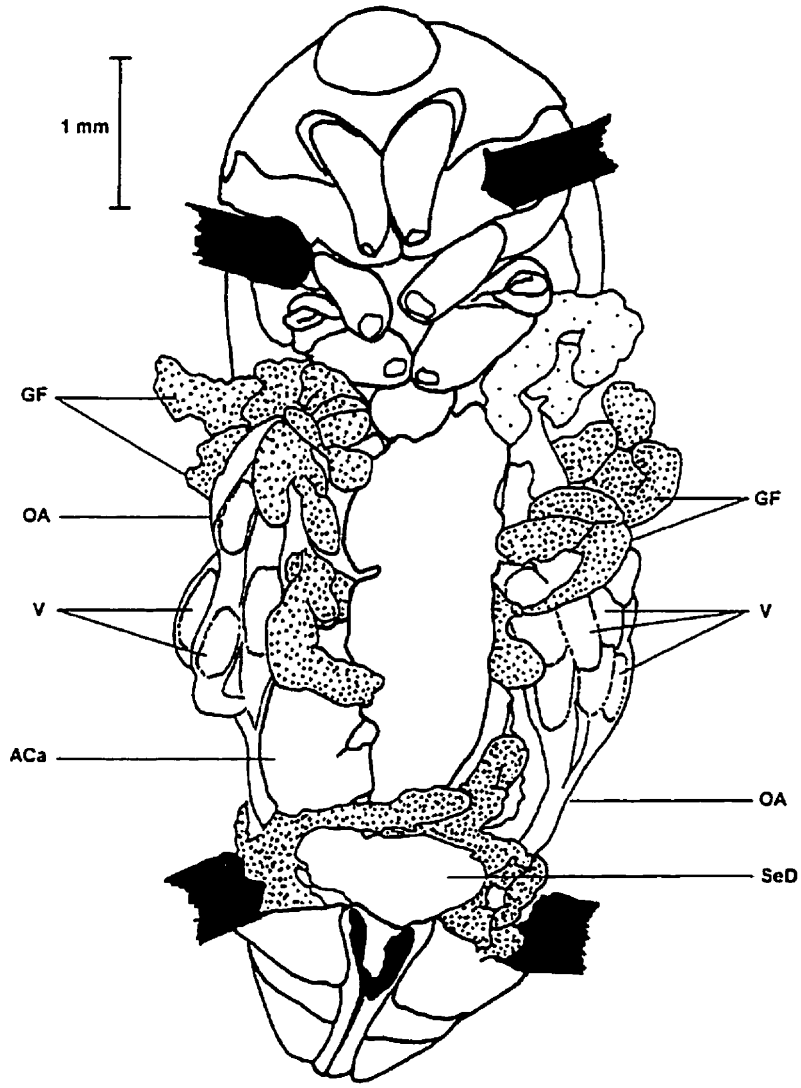
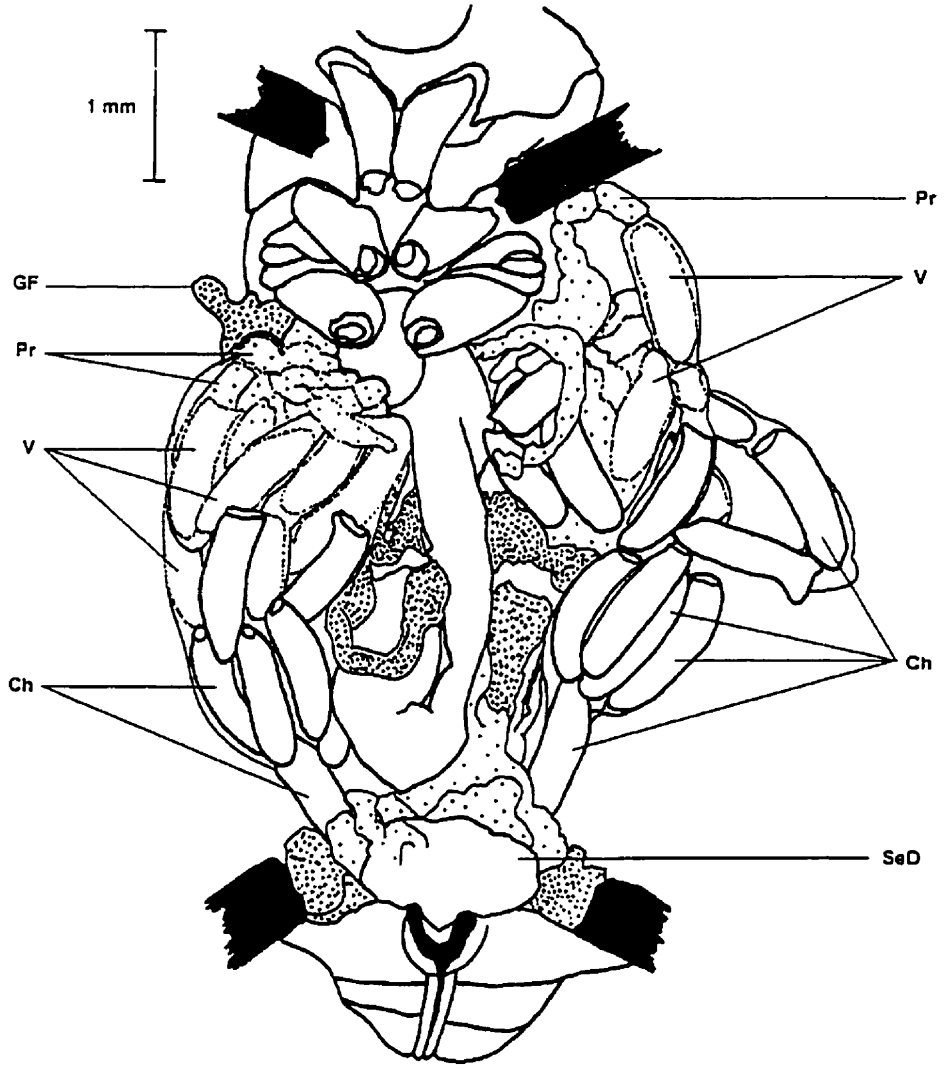

1 mm
GF
OA
V
ACa
GF
V
OA
SeD

Figure 7. *Lygus elisus* (Van Duzee) female with chorionated oocytes within her ovarioles (unmated 7-d-old).
Abbreviations: Ch, Chorionated oocyte(s). GF, Green fat bodies; Pr, Previtellogenic oocyte(s); SeD. Seminal depository; V, Vitellogenic oocyte(s).


1 mm
Pr
V
GF
Pr
V
Ch
Ch
SeD

3.3.2 Aging Field Collected Females

The age of field collected female *L. elisus* and *L. borealis* was estimated using age categories based on the reproductive status of colony reared *L. elisus* females.

Host Crops. *Lygus* were collected using a sweep-net from two crops, canola (*B. napus* L. cv. Westar) and sainfoin (*O. viciaefolia* Scop. cv. Nova), located on the Agriculture and Agri-Food Canada Lethbridge Research Centre farm near Lethbridge, Alberta. Canola treated with Vitavax Single™ (Carbathiin applied at a rate of 3 mL/kg) was seeded at 15 kg/ha into four stands on 11 May (77 m x 19.5 m), 14 June (63 m x 25 m), 14 June (101 m x 22.5m), and 12 July (101 m x 27 m). Each stand of canola was surrounded by a minimum 2 m plant-free boundary. The sainfoin crop, established in 1993, was divided into 3 stands (6.5 m x 87 m, 6.5 m x 87 m, 6.5 x 53 m) each of which was surrounded by a 5 m plant-free boundary.

Sweep-net Collections. The growth stage of individual canola stands was determined using the mode of 15 plants randomly sampled in a W-pattern in each stand (Harper and Berkenkamp 1975). Sampling commenced in canola stands at the rosette stage of development (2.0) and continued until early flowering (4.0). In the earliest seeded stand of canola, collections began on 11 May and were completed in the latest stand of canola on 26 August, prior to the end of early flowering at the bud stage (3.2). In sainfoin, sampling occurred over the same parts of the season as in the canola commencing on 14 June and completing on 26 August.

Sweep-net collections were performed in both crops using a 38 cm (dia.) net swept in 180° arcs through the canopy. Sweeping was performed between 10:30-13:00

hours. A W-pattern was followed to perform 100 sweeps through a stand of canola or sainfoin. In addition, a mass collection was performed over the entire stand of canola or sainfoin. Sampling was performed every second day in the canola stands but weekly in the sainfoin, weather permitting.

Sweep-net collected *Lygus* were killed by immersion in a dissecting solution of glacial acetic acid, formaldehyde, and chloral hydrate (Weaver and Thomas 1956) which also preserved specimens. *Lygus* adults were identified to species (Kelton 1983; Schwartz and Footitt 1992).

Aging Field Collected Lygus Females. The age of field collected *L. elisus* and *L. borealis* females was estimated based on laboratory dissections of unmated and mated colony reared *L. elisus* females (Section 3.3.1). Mating status, measured by the relative size of the seminal depository, and number of chorionated oocytes within a female' s ovarioles were the two variables used to estimate female age. The first variable, seminal depository size, was separated into four classes of relative size which was based on hypothesized changes in the size of the seminal depository that occur with mating then oviposition (uninflated, inflated, partly deflated, deflated) (Section 3.3.1). The second variable, number of chorionated oocytes, was separated into four classes based on dissections and observations of unmated and mated laboratory reared *L. elisus* females (0, 1-4, 5-17, >18 chorionated oocytes). Combinations of the two variables (4 classes x 4 classes) were used to form individual categories (total of 16 categories) to which approximate age was assigned.

Statistics. Chi-square (χ^2) 2 x 2 contingency tables were used to compare the

proportion of *L. elisus* females <7-days-old and >7-days-old collected in the canola and sainfoin and this was repeated for *L. borealis* females.

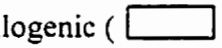
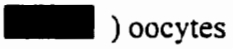
3.4 Results

3.4.1 Characterization of Female *Lygus elisus* Reproductive Status

Rearing difficulties affected the sample sizes obtained for dissection. Isolation of females and males resulted in high mortality. Of the over 250 females isolated in 3 years, 25 unmated females and 7 mated females were obtained for dissection.

Development of unmated females. Examinations of dissected, unmated females of varying age indicated that oogenesis does not begin until after adult eclosion (Fig. 8). In all unmated females examined in this study, the seminal depository was uninflated. Two-day-old unmated females (N=2) contained previtellogenic oocytes (Fig. 9). In a 4-day-old female (N=1) more of the ovarioles were occupied with previtellogenic oocytes (Fig. 5). At 5 days old (N=1), the ovarioles contained vitellogenic oocytes (Fig. 6). A seven day old female had chorionated oocytes within the ovarioles. In a 7-day-old female, a chorionated oocyte was visible within the lateral oviduct in the right and left sets of ovarioles in what was assumed to be preparation for oviposition (Fig. 7).

The number of chorionated oocytes in different aged unmated females varied (Fig. 8). Adult females 8-16 days old (N=9) contained the highest number of chorionated oocytes (43.0+4.61, 18-66, mean±SE, range, N=9) compared to females 2-7 days old (2.7+1.86, 0-14, N=7) and 39-53 days old (14.3+1.85, 9-19, N=4) (Fig. 8). Females older than 39 days contained fewer chorionated oocytes than younger females 8-16 days old

Figure 8. Mean number of vitellogenic () and chorionated () oocytes in colony reared, unmated and mated (*) *Lygus elisus* (Van Duzee) females of varying ages. Numbers above individual bars indicate the sample size at each age.

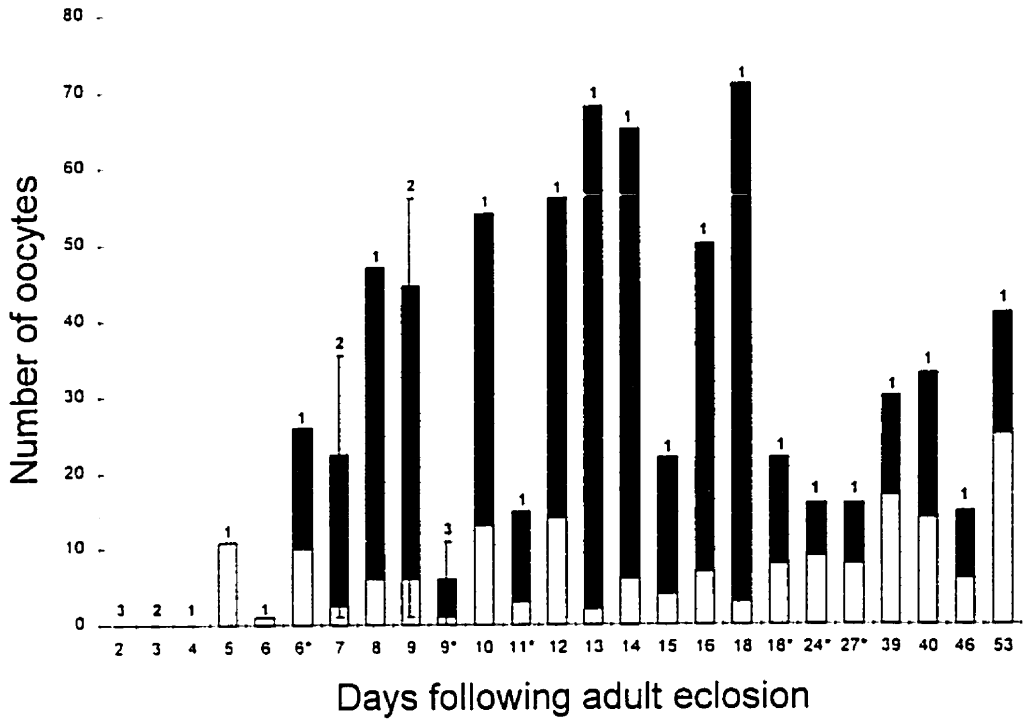
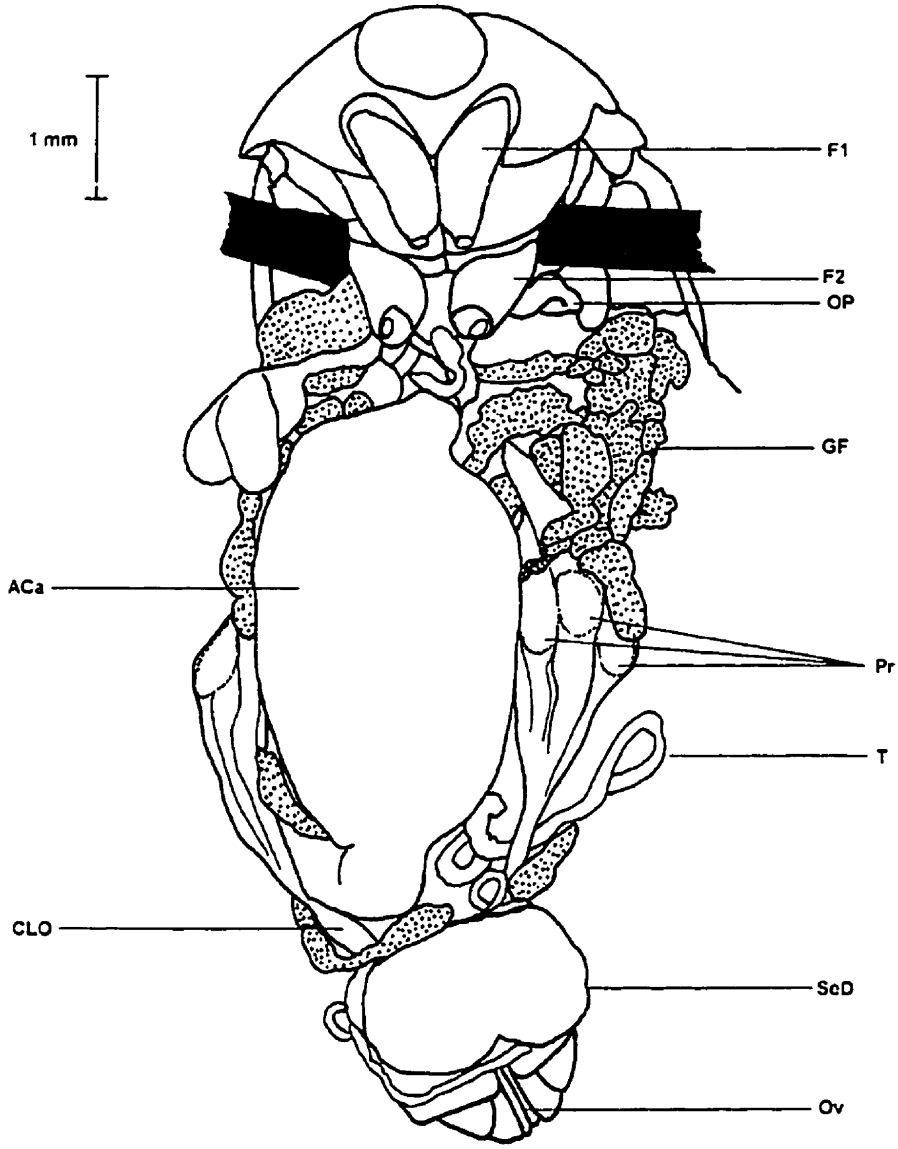

Number of oocytes
80
70
60
50
40
30
20
10
0
3 2 1
2 3 4 5 6 6* 7 8 9 9* 10 11* 12 13 14 15 16 18 18* 24* 27* 39 40 46 53
Days following adult eclosion

Figure 9. Unmated 2-d-old *Lygus elisus* (Van Duzee) female.
Abbreviations: SeD, Seminal depository.


1 mm
F1
F2
OP
GF
ACa
Pr
T
CLO
ScD
Ov

suggesting that older females, if they do not mate, absorb or dump oocytes, the latter of which occurs in unmated *L. hesperus* >9 days old (Strong et al. 1970). No oviposition occurred on stems of broccoli florets in the cages; however, the individual florets were not examined and may have contained eggs.

Development of mated females. The size of the seminal depository was divided into four relative sizes as observed in colony reared *L. elisus* and field collected *L. elisus* and *L. borealis* females which were dissected. The relative sizes were distinguishable in dissection by the degree of inflation and the colour of the organ which changed with copulation, receipt of male donated fluids, and use of the fluids. Storage of male fluids resulted in expansion of the seminal depository which lacks muscles (Davis 1955) and changes shape in a manner analogous to a balloon.

Just after mating, the seminal depository in *L. hesperus* became inflated and appeared as a white, smooth surfaced sac. The difference between an uninflated and deflated female was in the size of the translucent seminal depository. In colony reared *L. elisus* females, the seminal depository failed to return to the smaller size represented by the uninflated status. Inflated versus partly deflated seminal depository size was discernable by the difference in size of the enlarged, white organ. Thus, the progression of changes in the seminal depository, with mating, would logically follow that females had uninflated seminal depositories only when they are virgins. After an initial copulation, the seminal depository enlarged greatly and the normally translucent organ became opaque due to its contents. With time and use of the male donated fluids, the seminal depository became partly deflated but retained its white, opaque colour. The

seminal depository continued to shrink in size and became deflated, returning to its translucent appearance but never returned to the size of an uninflated seminal depository. Thus, the four relative sizes of the seminal depository which were used as the four classes to categorize field collected *Lygus* were individually distinguishable.

Based on dissections, mating and oviposition followed a pattern that began with the development of mature, chorionated oocytes within the ovarioles of the female. The oocyte complement (Fig. 8) and seminal depository size changed after mate pairings. In a mated 6-day-old female (N=1), ovarioles contained vitellogenic and chorionated oocytes and the seminal depository was greatly enlarged and characterized as partly deflated (Fig. 10). Few vitellogenic and no chorionated oocytes were present in ovarioles of mated 9-day-old females (N=3) relative to unmated females (N=2) (Fig. 8). No chorionated oocytes were present in the medial and posterior regions of the ovarioles or common lateral oviducts (Fig. 11 and Fig. 12). The ovarioles were distended and translucent but only the extreme anterior region of the ovarioles contained previtellogenic oocytes and the seminal depository was partly deflated. The egg complement of another 9-day-old female was similar, although, the seminal depository was deflated (Fig. 12). An absence of chorionated oocytes from the mated 9-day-old females suggests that one mating bout is sufficient for oviposition of all mature oocytes from the ovarioles. Dissection of a mated 11-day-old female (N=1) showed that females varied in their timing of oviposition as this female still contained several chorionated oocytes within its ovarioles and the seminal depository was partly deflated (Fig. 13). A mated 18-day-old female (N=1) had fewer vitellogenic and chorionated oocytes in her ovarioles relative to

Figure 10. Mated 6-d-old *Lygus elisus* (Van Duzee) female.
Abbreviations: SeD, Seminal depository.

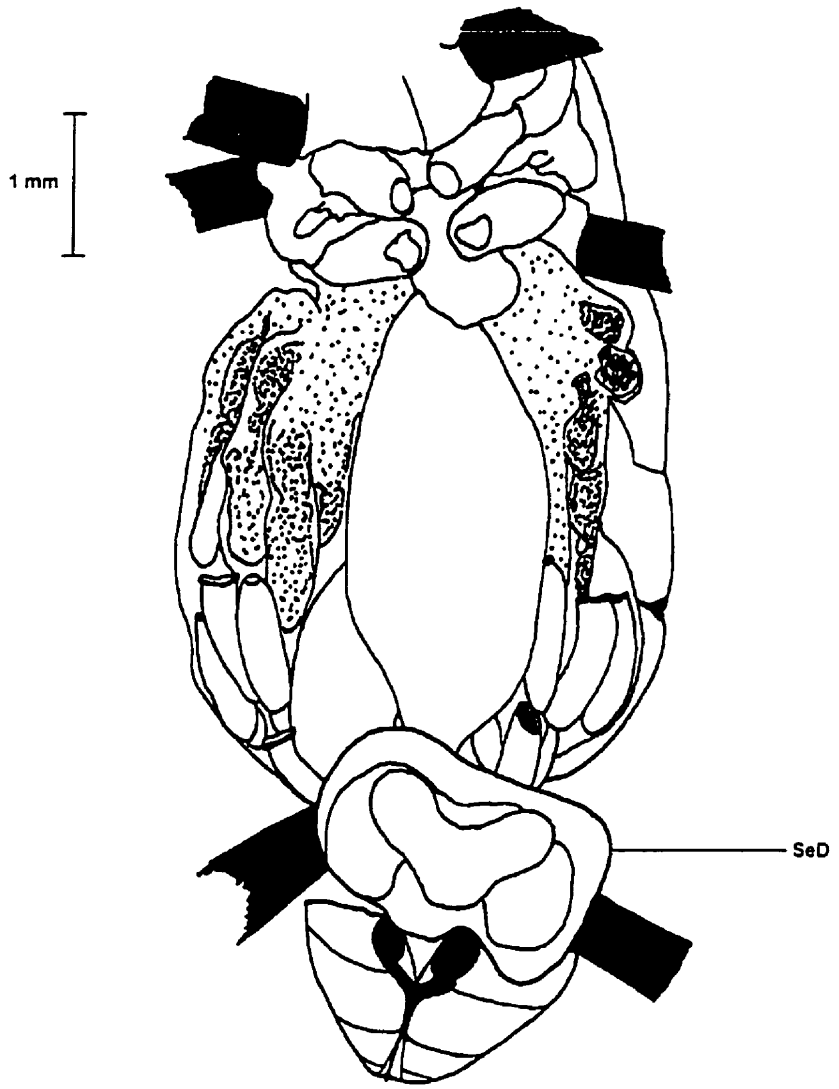

1 mm
SeD

Figure 11. Mated 9-d-old *Lygus elisus* (Van Duzee) female.
Abbreviations: SeD, Seminal depository.

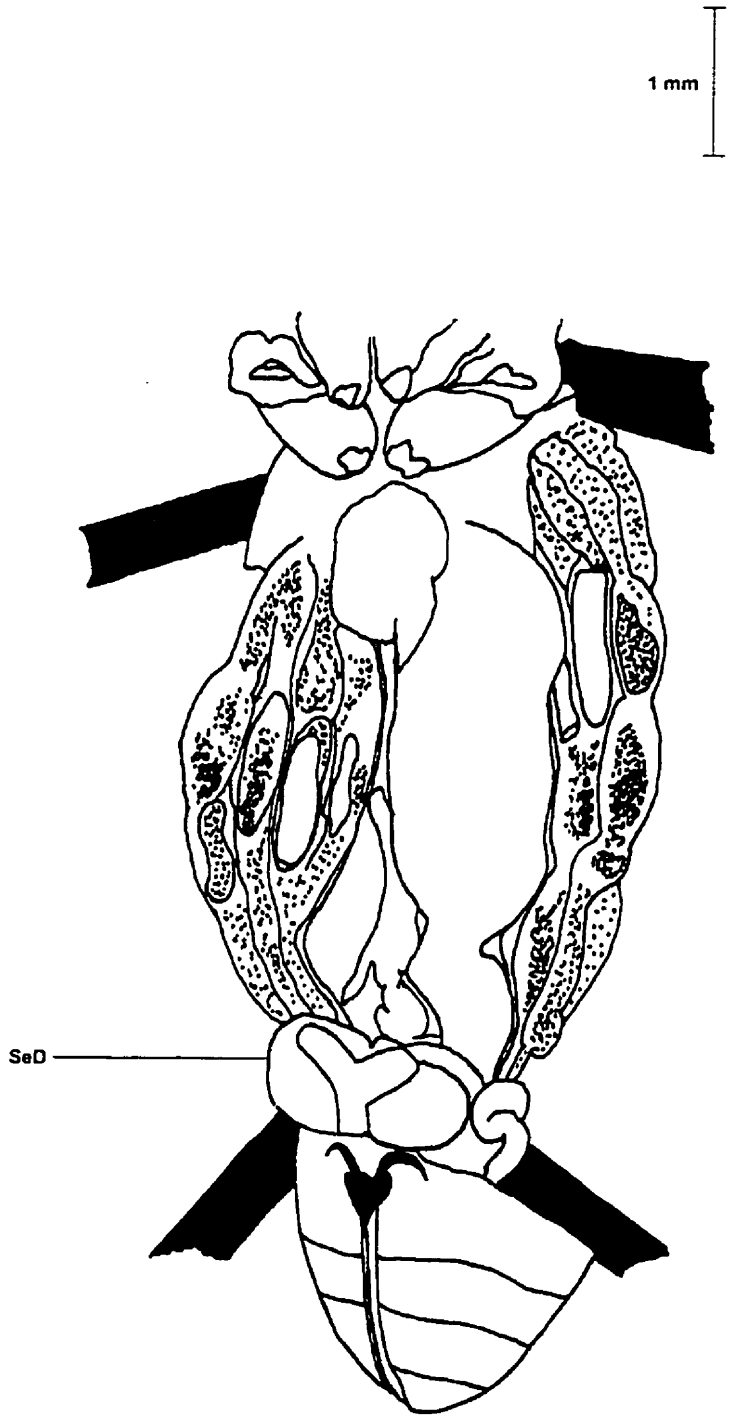

1 mm
SeD

Figure 12. Mated 9-d-old *Lygus elisus* (Van Duzee) female.
Abbreviations: SeD, Seminal depository.

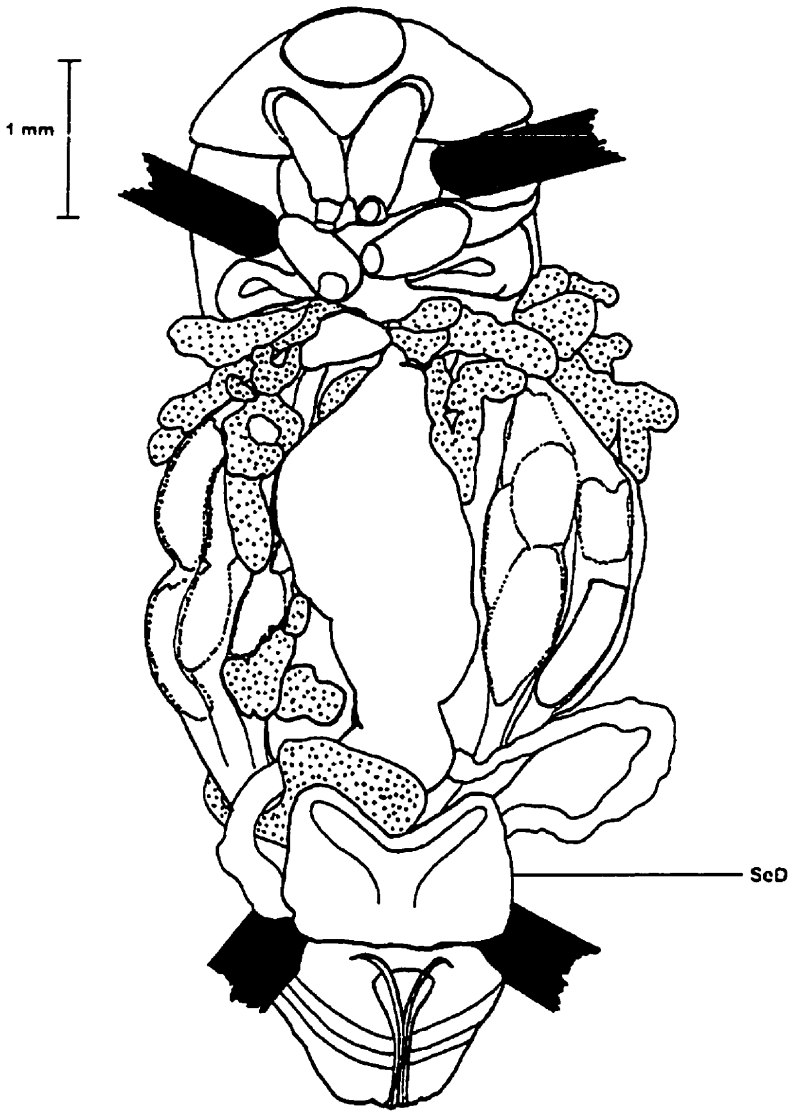
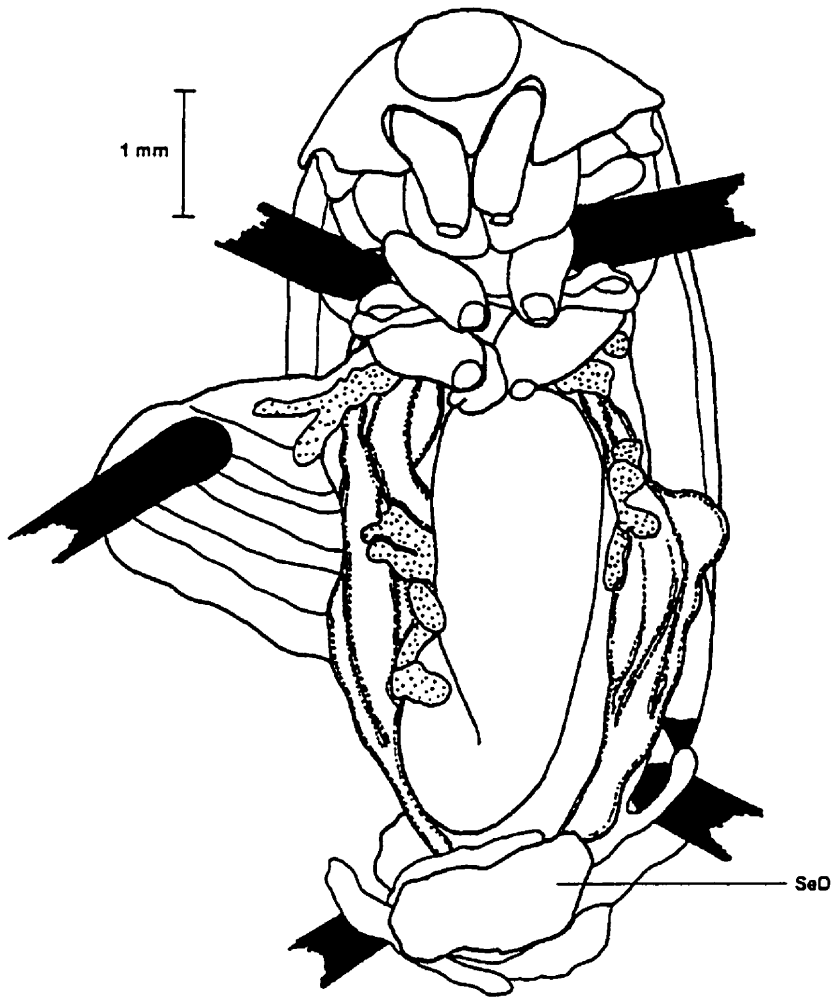

1 mm
ScD

Figure 13. Mated 10-d-old *Lygus elisus* (Van Duzee) female.
Abbreviations: SeD, Seminal depository.


1 mm
SeD

an unmated 18-day-old female (Fig. 8). The ovarioles in the mated 18-day-old female were distended but the seminal depository was enlarged and characterized as partly deflated (Fig. 14). Few vitellogenic or chorionated oocytes were observed in 24-day-old (N=1) and 27-day-old (N=1) mated females (Fig. 8) and their seminal depositories were inflated. The ovarioles in the 24-day-old and 27-day-old females were distended but no oocytes were visible in the posterior regions of the ovarioles nor in the common lateral oviducts (Fig. 15 and Fig.16, respectively) in contrast to unmated females 39, 40, 46, and 53 days old which contained a total of 13, 19, 9, and 16 chorionated oocytes in their ovarioles, respectively (Fig. 17, Fig. 18, Fig. 19, and Fig. 20).

3.4.2 Aging Field Collected Females

Field collected *L. elisus* and *L. borealis* females categorized as 1-5 days old, 6-7 days old, and >7 days old were present in canola and sainfoin fields (Table 2). Unmated females >7 days old , characterized by a seminal depository rating ≥3 and ≥18 chorionated oocytes in their ovarioles were rarely found (Table 2). Only 0.3% of females with chorionated oocytes were unmated (Table 2). None of the collected females fit into the relative reproductive development categories 10-15 which was characterize as having ≤4 chorionated oocytes but an inflated, partly deflated, or deflated seminal depository (Table 2). More young *L. elisus* and *L. borealis* females were present in the sainfoin than were present in the canola. Comparison of the proportions of *L. elisus* females ≤7 days and >7 days old between the canola and sainfoin indicated that high proportions of females in the canola were >7 days old (0.75) and low proportions were ≤7-days-old

Figure 14. Mated 18-d-old *Lygus elisus* (Van Duzee) female.
Abbreviations: SeD, Seminal depository.

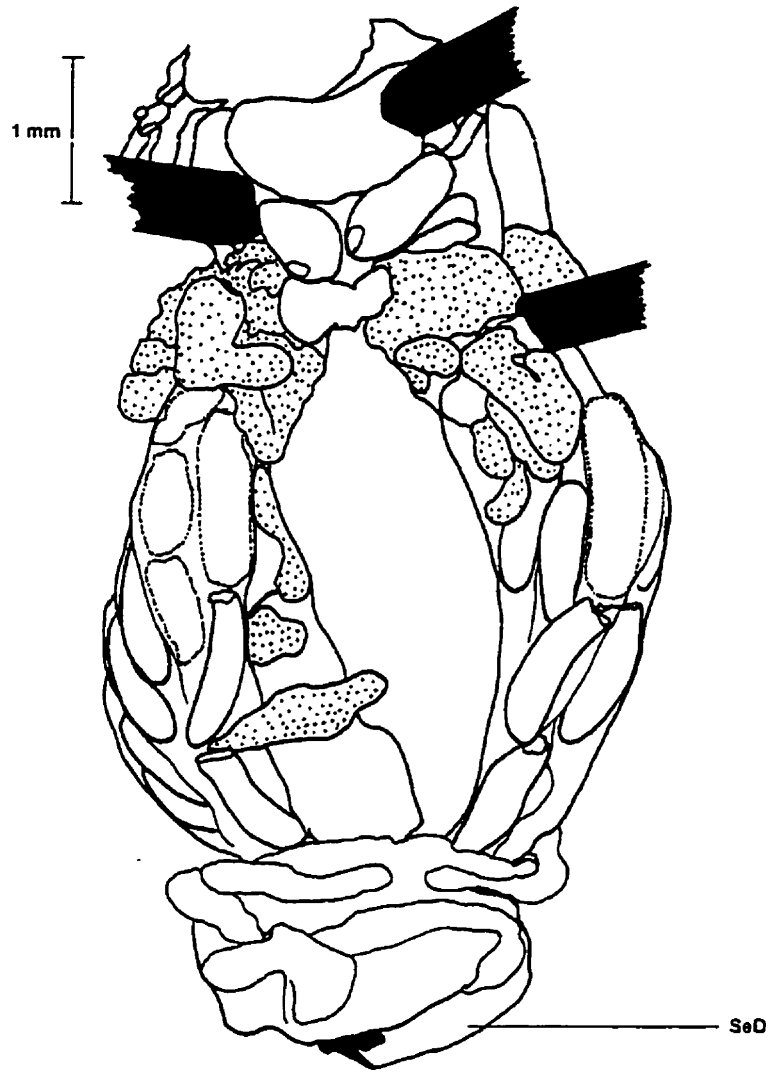

1 mm
SeD

Figure 15. Mated 24-d-old *Lygus elisus* (Van Duzee) female.
Abbreviations: SeD, Seminal depository.

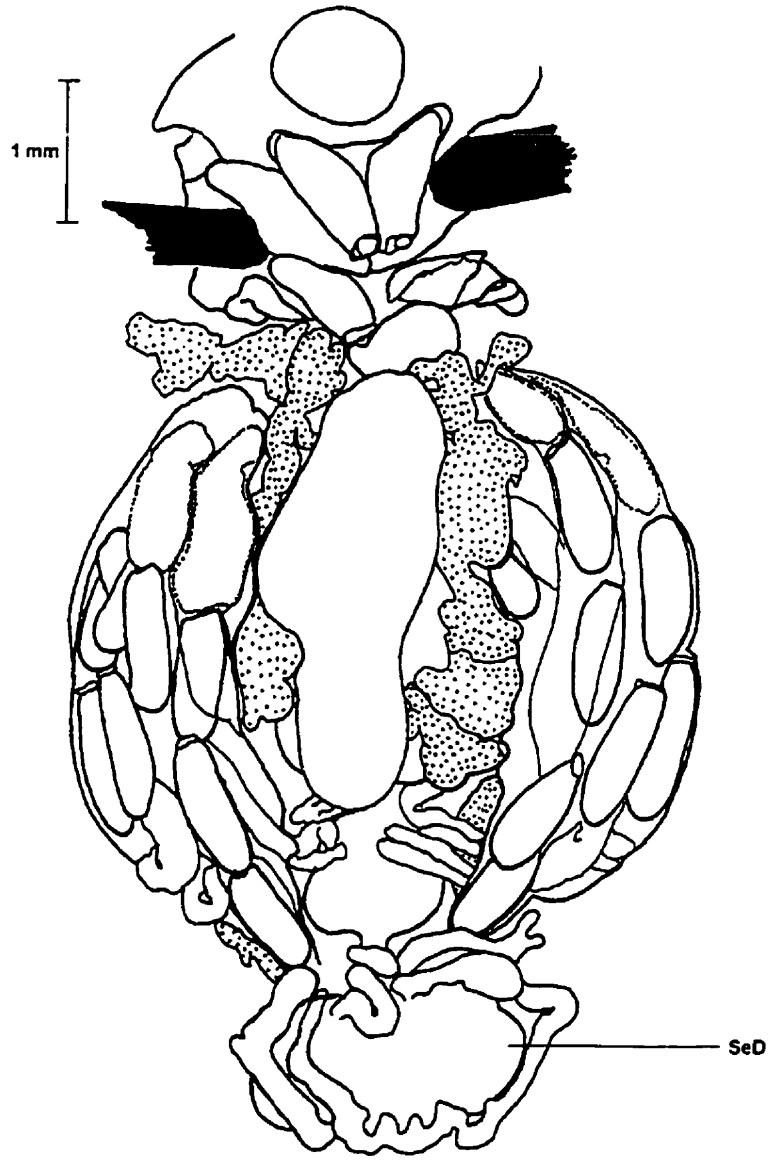

1 mm
SeD

Figure 16. Mated 27-d-old *Lygus elisus* (Van Duzee) female.
Abbreviations: SeD, Seminal depository.

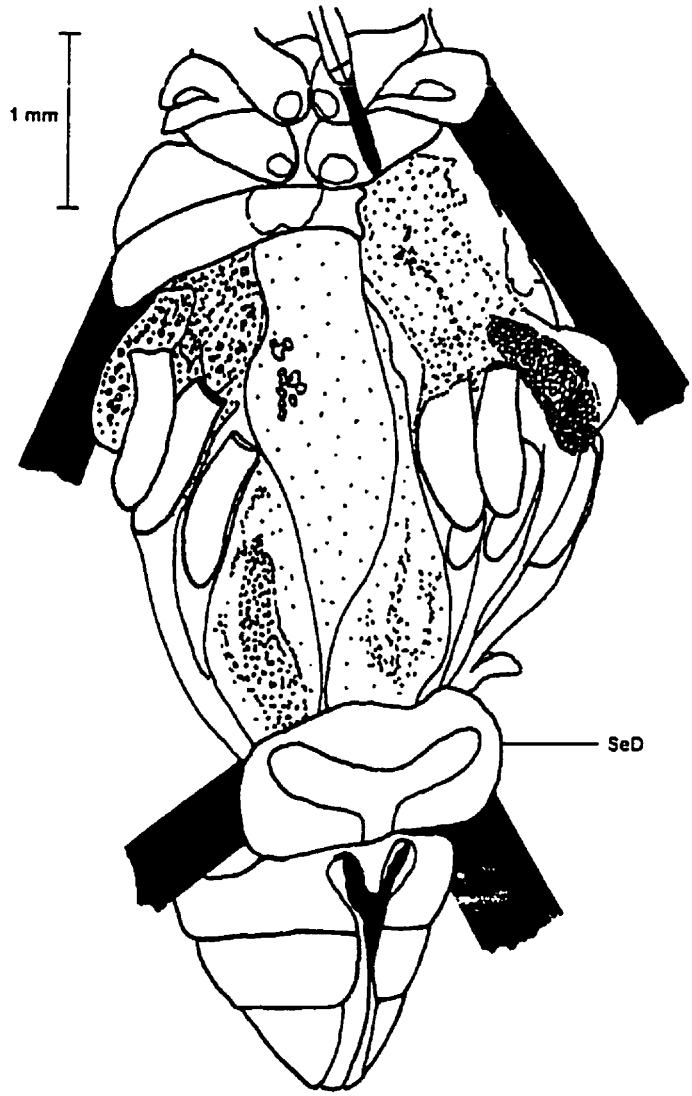

1 mm
SeD

Figure 17. Unmated 39-d-old *Lygus elisus* (Van Duzee) female.
Abbreviations: SeD, Seminal depository.

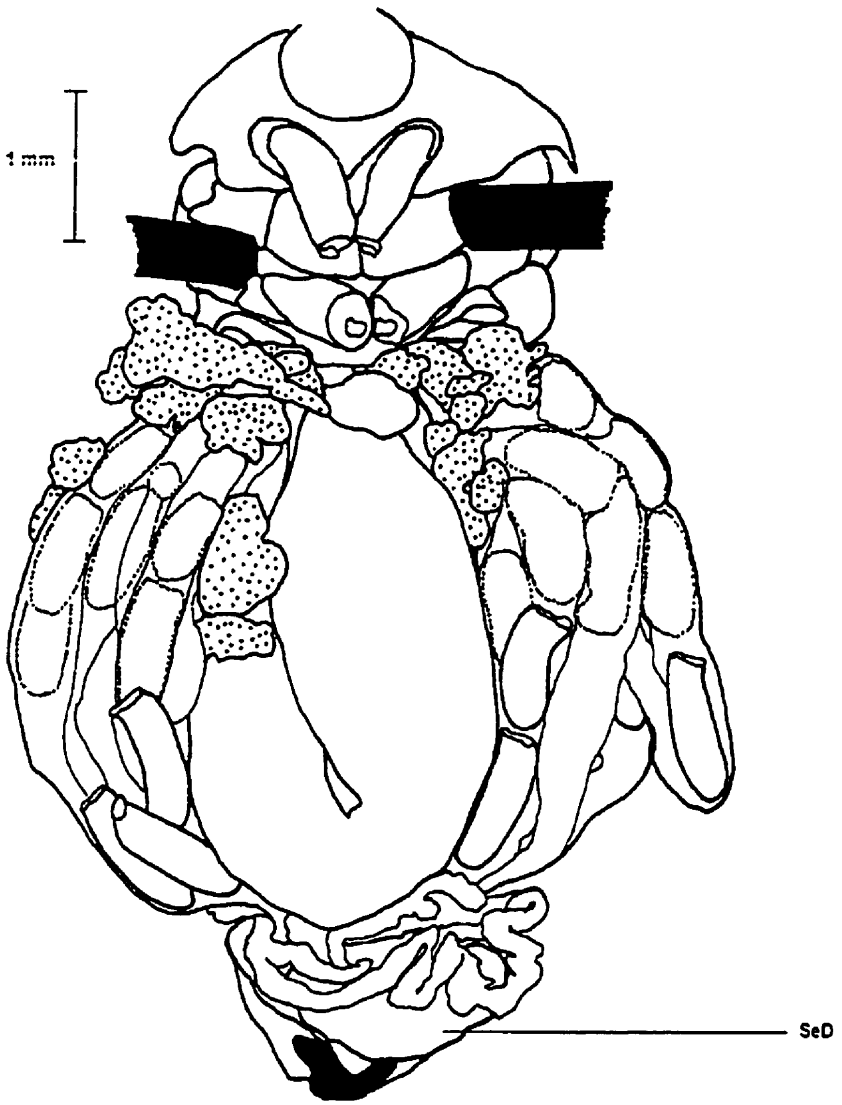

1 mm
SeD

Figure 18. Unmated 40-d-old *Lygus elisus* (Van Duzee) female.
Abbreviations: SeD, Seminal depository.

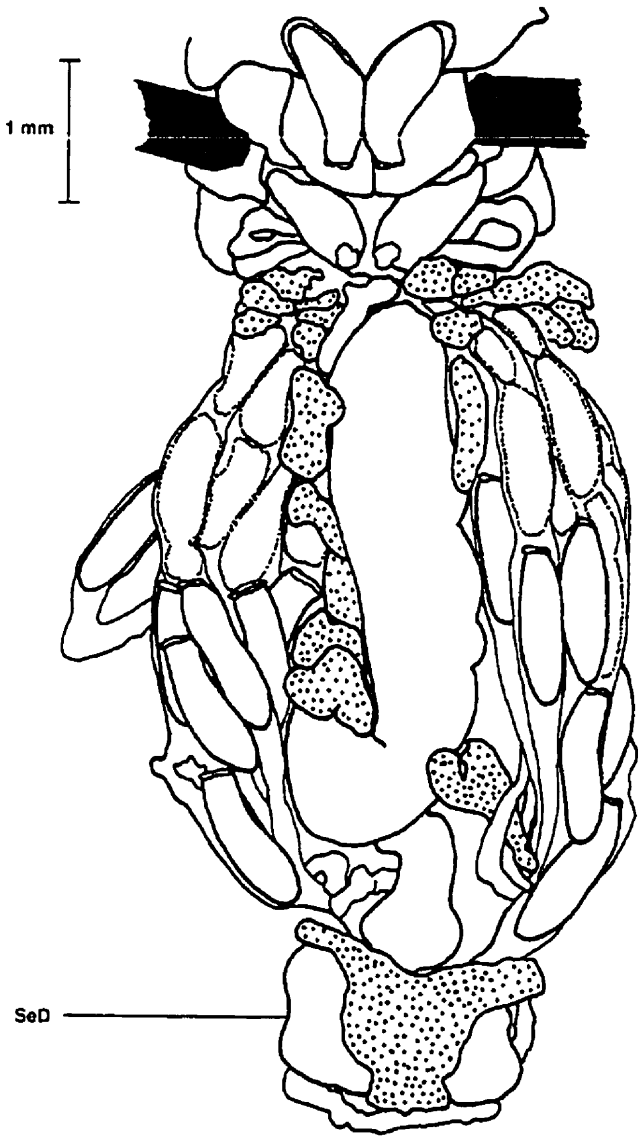

1 mm
SeD

Figure 19. Unmated 46-d-old *Lygus elisus* (Van Duzee) female.
Abbreviations: SeD, Seminal depository.

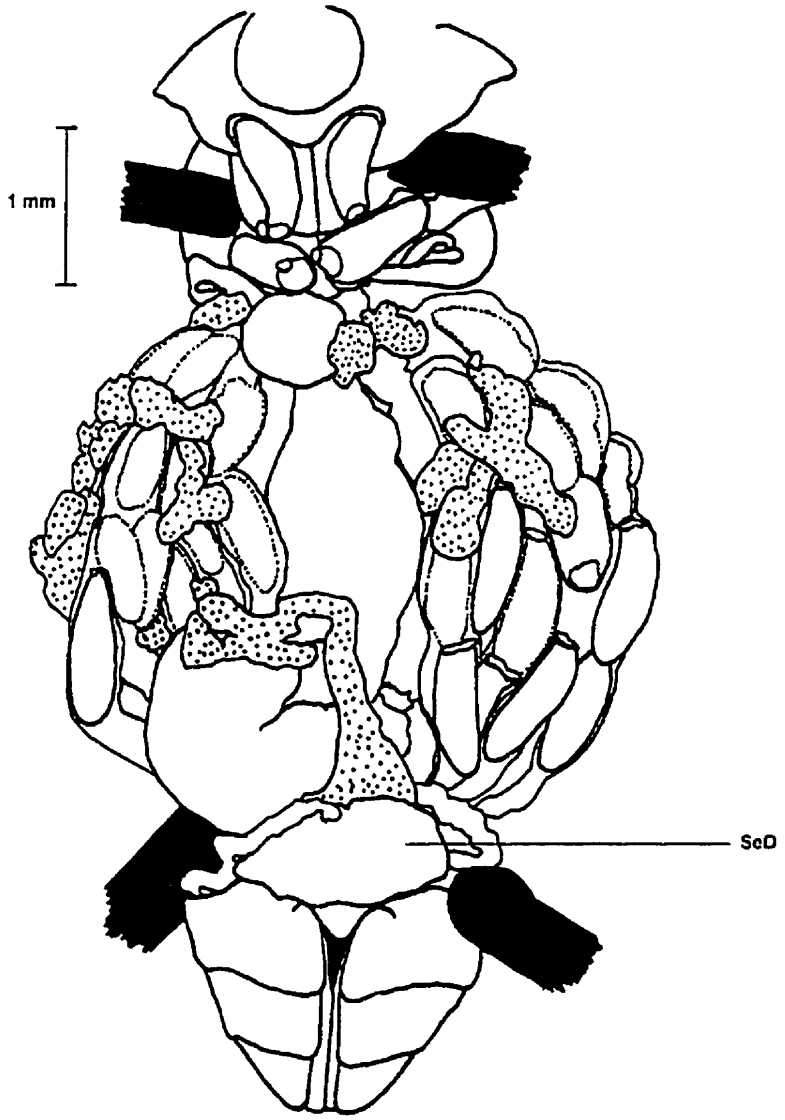

1 mm
ScO

Figure 20. Unmated 53-d-old *Lygus elisus* (Van Duzee) female.
Abbreviations: SeD, Seminal depository.

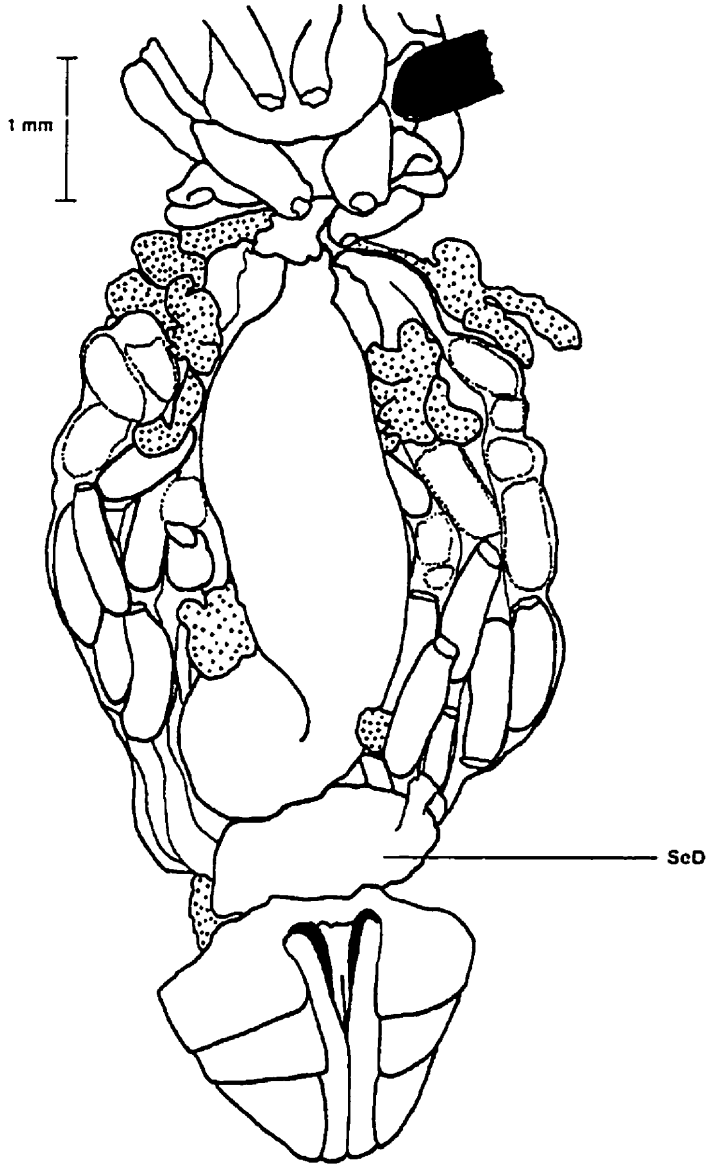

1 mm
ScD

Table 2: Total number of *Lygus elisus* and *L. borealis* females in hypothesized age categories randomly sweep-net collected from canola (*Brassica napus* L. cv. Westar) and sainfoin (*Onobrychis viciaefolia* Scop. cv. Nova) stands from 14 June - 26 August in 1995.

Relative reproductive development categories	Size of seminal depository	Number of chorionated oocytes	Category characteristics	Hypothesized age after eclosion	Total number of females				TOTALS
					Canola		Sainfoin		
					L. elisus	*L. borealis*	*L. elisus*	*L. borealis*	
1	unin flated	0	Unmated, non-reproductive	1-5d old	204	134	195	575	1108
2	unin flated	1-4	Unmated, pre-oviposition	6-7d old	1		2		3
3	unin flated	5-17	Unmated, pre-oviposition	6-7d old	1	1	1	1	4
4	unin flated	>18	Unmated, pre-oviposition	>7d old		2			2
5	in flated	>18	Mated, pre-oviposition	>7d old	185	342	17	60	604
6	partly deflated	>18	Mated, pre-oviposition	>7d old	56	174	5	53	288
7	in flated	5-17	Mated, ovipositing	>7d old	9	12	2	2	25
8	partly deflated	5-17	Mated, ovipositing	>7d old	301	390	30	86	807
9	deflated	5-17	Mated, ovipositing	>7d old	118	135	9	70	532
10	in flated	1-4	Mated, ovipositing	>7d old					0
11	partly deflated	1-4	Mated, ovipositing	>7d old					0
12	deflated	1-4	Mated, ovipositing	>7d old					0
13	in flated	0	Mated, post-ovipositional	>7d old					0
14	partly deflated	0	Mated, post-ovipositional	>7d old					0
15	deflated	0	Mated, post-ovipositional	>7d old					0
16	deflated	>18	Mated, pre-oviposition	>7d old					0
				TOTALS	875	1190	261	847	3373

(0.24), whereas, high proportions of females in the sainfoin were ≤7 days old (0.76) and low proportions were >7 days old (0.24) (χ^2=248.53, df=1, p<0.01). In *L. borealis*, very high proportions of females were >7 days old (0.90) and low proportions of females were ≤7 days old (0.10) in the canola whereas in the sainfoin, high proportions of females were ≤7 days old (0.68) and low proportions of females were >7 days old (0.32) (χ^2=907.98, df=1, p<0.01).

Significantly different proportions of ≤7 day old and >7 day old female *L. elisus* and *L. borealis* were present in the sainfoin (χ^2=596.82, df=1, p<0.01). High proportions of *L. elisus* were categorized as ≤7 day old (0.76) and relatively lower proportions were categorized as >7 day old (0.24) in the sainfoin. Similarly, high proportions of *L. borealis* were categorized as ≤7 day old (0.68) while relatively low proportions were > 7 day old (0.32). In the canola, significantly different proportions of *L. elisus* and *L. borealis* females were categorized as ≤ or > 7-days-old (χ^2=192.09, df=1, p<0.01). Low proportions of *L. elisus* females were categorized as ≤7 days old (0.24) and relatively higher proportions were categorized as > 7 days old (0.76). Similar to *L. elisus*, low proportions of *L. borealis* were categorized as ≤7 days old (0.10) and relatively high proportions of were categorized as > 7 days old (0.90). High proportions of both *L. elisus* and *L. borealis* females were categorized as ≤7 days old in the sainfoin while high proportions of both *L. elisus* and *L. borealis* were categorized as > 7 days old in the canola.

3.5 Discussion

3.5.1 Characterization of Female *Lygus elisus* Reproductive Status

Lygus hesperus (Strong et al. 1970) mate multiple times. Strong et al. (1970) recorded *L. hesperus* females mating up to three times. In this study, dissections from unmated female *L. elisus* revealed no more than 70 chorionated oocytes in the ovarioles whereas Gerber (1995) recorded fecundity of overwintered and first generation *L. lineolaris* to range between 250-334 nymphs per female. If *L. elisus* females contain approximately 70 oocytes per egg complement and experience 3 or 4 matings, *L. elisus* might approach the fecundity for *L. lineolaris* observed in the field (Gerber 1995).

Mated *L. elisus* females which have oviposited their first fully chorionated oocytes retained a previtellogenic area in the extreme anterior region of the ovarioles. This region is the likely source of subsequent complements of mature oocytes developed during a recovery period. Strong et al. (1970) noted that after mating occurs in *L. hesperus*, there is a recovery period where females are not receptive to males nor do they oviposit. It is possible that this recovery period is terminated by oogenesis in the anterior regions of the ovarioles and subsequent production of mature oocytes which trigger female receptivity to mating. If *L. elisus* and *L. lineolaris* fecundity is similar, chorionated oocytes oviposited would be replaced by subsequent development of more chorionated oocytes.

Dissections of unmated female *L. elisus* revealed an important finding that egg development occurred independent of and prior to mating. The production of chorionated oocytes in unmated female *L. elisus* at six days approximates the seven day

pre-reproductive period Strong et al. (1970) found in *L. hesperus*. Chorionated oocyte production is required before mating can occur and mating does not initiate oogenesis.

If mating does not occur within 7 days of female adult eclosion, chorionated oocytes continue to be produced within the ovarioles. After 16 days the number of chorionated oocytes decreased in unmated females due either to dumping or absorption of oocytes. Reduction in oocytes may result in lowering female weight which may make movement easier. As well, absorption of oocytes might reallocate energy to allow movement or to prolong life.

3.5.2 Aging Field Collected Females

Based on laboratory dissection, it was hypothesized that 16 discrete age categories of *Lygus* females can be identified. These were characterized by combinations of four discrete stages of inflation of the seminal depository and four levels of chorionated eggs. The four categories of inflation of the seminal depository were based on the hypothesis that the seminal depository reaches the maximum size just after mating and then shrinks as the seminal fluid is used. Thus the seminal depository is initially uninflated and maximum inflation occurs with mating (inflated) with shrinkage occurring over time (partially deflated and deflated). In the laboratory, females developed chorionated oocytes which numbered from 0 up to >18 and these were divided into four discrete categories (0, 1-4, 5-17 and >18 chorionated oocytes).

Uninflated was a category of the seminal depository that applied to only the very young females who had never mated. These were common in the field. Most of the

unmated females (99.1%) collected in the field had no chorionated eggs, which, from laboratory studies, made them less than 7 days old (category 1, Table 2). Females in categories of non-mated with chorionated oocytes (categories 3-5, Table 2) did exist, but they were rare indicating that these stages are very short-lived with mating occurring very quickly after chorionated oocytes develop at about 6-7 days of age.

After mating the seminal depository becomes fully inflated and a female carries a full complement of eggs before ovipositing. This category (5, Table 2) was found commonly in the field. The category following this (6, Table 2), with a partially deflated seminal depository plus a full complement of eggs, is less common but also frequently collected in the field.

The first six categories discussed here are discrete and progressive indicating that it is possible to categorize females into six distinct age-related classes up to the point of first oviposition in the field. Reproductive stages after this become much more difficult to differentiate.

It is evident that females collected in categories 7 to 9 are older than those classified in stages 1-6 because they are actively ovipositing and their egg complement is reduced. However the change from category 7 to 9, although discrete, may not be related to increasing female age. From category 7 to category 9 the seminal depository shrinks. This shrinkage would be associated with increasing age if the females mated only once but other studies indicate that multiple mating occurs in *Lygus* (Strong et al. 1970). Therefore, one cannot say with certainty that these categories occur sequentially as the females age.

Categories 10 to 16 are based on the hypothesis that as females age, the number of chorionated eggs will decline to zero and eventually the females will age past a point where they are able to oviposit. As well, because multiple mating occurs, older females in various categories of inflation of the seminal depository should also be found in the field. However, no females in any of these categories were collected in the field. This indicates that females do not oviposit their full complement of eggs and categories 10-16 are not valid for establishing the age of females collected in the field.

3.5.3 Patterns of Reproduction in Field Populations

The reduction in size of the seminal depository was not related to a decline in egg numbers in mated females. For example, many of the females collected had fewer than 18 eggs, which indicated that they were actively ovipositing, but had a fully inflated seminal depository. Therefore, these females had taken on more sperm fluid after many chorionated eggs had been oviposited. This indicates that the females were mating more than once during the collection period of this study. This finding agrees with laboratory studies conducted with *L. hesperus* where females were observed multiple mating (Strong et al. 1970).

If we assume multiple mating occurs in *L. elisus and L. borealis*, reproductive development may be hypothesized to follow one of two patterns. (i) Initial mating occurs when a full complement of chorionated oocytes is developed within a female's ovarioles. The batch is then depleted and a new batch of oocytes is produced at which time mating reoccurs. (ii) An initial mating occurs only after a full complement of chorionated

oocytes is present within a female's ovarioles with subsequent mating occurring when required and chorionated oocytes are produced continuously and oviposited as they develop.

In both hypotheses the initial mating does not occur until a number of chorionated oocytes are present (>18 chorionated oocytes) within a female's ovarioles. Mating occurs and the female begins to oviposit chorionated oocytes. The two hypotheses differ at the point when subsequent mating occurs in relation to the female's production of chorionated oocytes.

In hypothesis (i), all available chorionated oocytes are depleted through oviposition then a new complement of chorionated oocytes is produced. Mating follows the production of a new batch of chorionated oocytes and, once again, all available chorionated oocytes are oviposited. Eventually, when the female draws to the end of her reproductive life, the available chorionated oocytes are depleted from her ovarioles and she dies.

In hypothesis (ii), following the initial mating event, the female begins to oviposit chorionated oocytes. Oocytes are not produced in batches. As eggs are oviposited, the female begins to produce more chorionated oocytes, continuously maintaining chorionated oocytes within her ovarioles. During this time, the female is receptive to subsequent mating events which provide sperm to fertilize the continuous production of oocytes.

Upon examining the two hypotheses for *Lygus* multiple mating, the absence of mated females with <5 chorionated oocytes (categories 10-16, Table 2) suggests that full

complements are not oviposited by female *L. elisus* or *L. borealis* as was suggested in hypothesis (i). None of the field collected *L. elisus* or *L. borealis* ever contained less than 5 chorionated oocytes. Instead, according to hypothesis (ii), chorionated oocytes appear to be continually produced in the female's ovarioles once oviposition begins and female's do not deplete chorionated oocytes from their ovarioles, dying with at least 5 chorionated oocytes in their ovarioles.

To summarize, *L. elisus* females develop chorionated oocytes independent of mating. Unmated females developed many chorionated oocytes prior to mating. The development of chorionated oocytes occurred very quickly. Female *L. elisus* <6 days old did not contain chorionated oocytes but females >7 days old contained a minimum of 18. Mating results in the expansion of the seminal depository and a decrease in the complement of chorionated oocytes. One mating is sufficient for oviposition of all chorionated oocytes in colony reared *L. elisus*. However, field collected females never deplete chorionated oocytes within ovarioles. This study was not able to determine how long females live or how many times they mated. However, it was evident from field collections that multiple mating was occurring. The proposed age categories successfully differentiated females ≤7 days old, and separated these females from those that were >7 days old. However, division into discrete age categories of females older than 7 days will require more detailed studies.

Further information regarding the reproductive development of *Lygus* may be very useful. However, laboratory rearing methods need to be improved in order to study further multiple mating and the later stages of a *Lygus* female's reproductive life. Female

fecundity, mating habits, and the association between mating and oviposition for other *Lygus* species may be different and deserves further study.

4. REPRODUCTIVE BIOLOGY OF *LYGUS ELISUS* (VAN DUZEE) AND *LYGUS BOREALIS* (KELTON) (HETEROPTERA: MIRIDAE) COLLECTED BY SWEEP-NET FROM CANOLA (CRUCIFERAE: *BRASSICA NAPUS* L. CVS. LEGEND, WESTAR) AND FORAGES (LEGUMINOSAE: *MEDICAGO SATIVA* L. AND *ONOBRYCHIS VICIAEFOLIA* SCOP. CV. NOVA).

4.1 Abstract

A study was conducted to determine the reproductive status of *Lygus* infesting canola and forage crops in southern Alberta. Sweep-net collections of *L. elisus* and *L. borealis* were performed in annually seeded canola and perennial forage crops from days 172 to 210 in 1994 and days 131 to 216 in 1995 in Lethbridge, Alberta. The ratio of males to females, the female mating status, and the status of egg development for *L. elisus* and *L. borealis* were determined.

Comparison of *L. elisus* and *L. borealis* sex ratios during identical sampling periods in canola and forage crops indicate that sex ratios varied in both species and between years. Sex ratios observed for *L. elisus* and *L. borealis* fluctuated through the study period. However, for both *L. elisus* and *L. borealis* species, mating status differed depending on the crop. High frequencies of mated females were collected from the canola while high frequencies of unmated females were collected in the forage crops. In canola, many females contained vitellogenic or chorionated oocytes ready for oviposition while in forages few females contained oocytes in these stages over the same period. Most of the females of both species in the forage contained previtellogenic oocytes not

yet ready for oviposition. Therefore, *L. elisus* and *L. borealis* females were reproductively mature in canola but reproductively immature in forages. These results suggest that *L. elisus* and *L. borealis* are younger in the forage compared to those in the canola during identical sampling periods, that females utilize canola and forage crops differently based on the completion of reproductive activities, and that both species exhibit a movement pattern where reproductively mature females participate in movement.

4.2 Introduction

Lygus are polyphagous insects (Kelton 1983) which are highly dispersive as adults and nymphs (Stewart and Gaylor 1994a). Every year, varying densities of a number of *Lygus* species are present on numerous host crops (Section Two). *Lygus* feed preferentially on the meristematic tissues of host plants which results in damage to the newly forming buds, flower and seeds (Hori 1974). On some hosts, *Lygus* cause considerable economic damage and warrant control measures which presently consist of chemical applications (Wise and Lamb 1998). During a growing season, a single species of *Lygus* has been recorded on several species of plants which develop and mature at different times (Cleveland 1982; Fye 1980). Common species of weeds form a sequenced host series for *Lygus* throughout the season (Fye 1980).

In southern Alberta, Salt (1945) recorded three generations of *Lygus* adults in alfalfa (*Medicago sativa* L.) within a growing season. Adults overwinter and emerge in early spring followed by an adult peak in mid-July and another adult peak in late-

September (Salt 1945). *Lygus* are found in canola (*Brassica napus* L.), a crop commonly grown in the Canadian prairie provinces. The *Lygus* found in annually sown canola result from adult dispersal, likely after a generation has been completed on other hosts (Leferink and Gerber 1997). Adult *Lygus* dispersal to canola commences at the rosette canola crop stage with major increases in *Lygus* populations occurring at the bud to flower stages of canola (Butts and Lamb 1991; Gerber and Wise 1995; Leferink and Gerber 1997). *Lygus* dispersal to canola is widely believed to be the result of the feeding requirements of adults, although it is not known why *Lygus* move or why they disperse to hosts like canola.

The need for mating opportunities and oviposition should also be considered in understanding *Lygus* dispersal to canola. Ridgeway and Gyrisco (1960) found that the average sex ratio from sweep-net collections of *L. lineolaris* in birdsfoot trefoil (*Lotus corniculatus* L.) is male biassed over the growing season. *Lygus lineolaris* colonizing mustard (*Brassica juncea crispifolia* L.) exhibit a sex difference in flight patterns (Stewart and Gaylor 1991). Males make more trivial flights while females make directed and dispersive flights (Stewart and Gaylor 1991). Young adults are more inclined to colonize mustard than older adults, colonizing females are older than males, and <10% of these females are unmated.

Fecundity has been examined for certain species of *Lygus*. Gerber (1995) estimated fecundity of overwintered and first-generation adult female *L. lineolaris* by determining nymph production. Oviposition was estimated to last between 5-7 weeks for both adult generations with production of approximately 281±34 nymphs per female

(range of 6-704 nymphs) (Gerber 1995).

Oviposition preferences have been studied in caged and laboratory *Lygus*. Gerber (1997) found that *L. lineolaris* differentiate between two cruciferous genera of *Brassica* and *Sinapis*. *Lygus lineolaris* choose *Sinapis* then later oviposit on *Brassica* (Gerber 1997). *Lygus lineolaris* oviposit preferentially on *S. alba* compared to *S. arvensis* thus a genus and species preference was exhibited between the plants tested (Gerber 1997). Stewart and Gaylor (1994b) found that *L. lineolaris* oviposition is higher on fleabane (*Erigeron strigosus* Muhlenberg ex. Willdenow) compared with cotton (*Gossypium hirsutum* L.). Benedict et al. (1983) found that *L. hesperus* oviposition, estimated by egg count, differs between three levels of trichome density and that the leaf petiole, particularly the pulvinus, is the preferred oviposition site on the host plant. The highest total number of eggs are oviposited on cotton plants with short, dense trichomes compared to plants with glabrous, trichome-free leaves, or medium length, normal density trichomed leaves (Benedict et al. 1983).

Field studies have been conducted to examine the seasonal reproductive status of female *Lygus* collected from various hosts. Gerber and Wise (1995) examined the egg development of female *L. lineolaris* collected from strawberry (*Fragaria* x *ananassa* Duchesne), and alfalfa (*Medicago sativa* L.) fields in southern Manitoba. They compared the frequencies of females with previtellogenic, vitellogenic, and chorionated eggs contained in the ovarioles. Egg development changed throughout the season in three successive years where overwintered females had chorionated oocytes from mid-May to mid-June, from mid-June to early August first generation females had various stages of

oocytes, then from mid-August to late September second generation females had chorionated oocytes. Oocyte development in these three periods each season was attributed to the progression of egg development in two generations of females in these two crops. Stewart and Gaylor (1991) used a spectrophotometer to measure light transmittance of hemelytra of individual adults to determine age of *L. hesperus* colonizing mustard (*Brassica juncea crispifolia* L.) and reported that young adults are more inclined to colonize a new patch of mustard than old adults. Colonizing females are generally older than males and the older age suggests that these females are largely parous. Only 6.6% of the females colonizing the mustard are unmated judging by the size of the seminal depository (Stewart and Gaylor 1991).

Lygus dispersal may be an adaptation for locating mates, a suitable food source, or in the case of females, suitable oviposition sites. This study compares *L. elisus* and *L. borealis* adults in canola and forage stands during identical sampling periods to determine if the sex ratios, female mating status, and female egg development status is different in these two crops.

4.3 Materials and Methods

Lygus host crops

Canola was seeded in 1994 (*Brassica napus* L. cv. Legend) and 1995 (*B. napus* L. cv. Westar) into fields located on the Agriculture and Agri-Food Canada Lethbridge Research Centre farm near Lethbridge, Alberta. All canola seed was treated with a fungicide treatment, Vitavax Single™ (Carbathiin at a rate of 3 ml/kg), to control

seedling blight, and then seeded at a rate of 15 kg/ha.

In 1994, canola (*B. napus* cv. Legend) was seeded on 11 May and 14 June into two plots (37 m x 57 m) separated by a 2 m plant-free border. A triangular forage field (base 140 m x height 200 m x 0.5), located 400 m south of the two canola stands, was selected for comparison collections of *Lygus*. The forage crop was alfalfa (*Medicago sativa* L.) used for silage and was more than 8 years old.

In 1995, canola (*B. napus* cv. Westar) was seeded 11 May (77 m x 19.5 m) and 14 June (63 m x 25 m) into two plots separated by a 2 m plant-free border. The cultivar Westar was used instead of Legend because no insecticide-free Legend could be purchased. A forage field selected for comparison collections was located 60 m south of the canola. The forage crop was sainfoin (*Onobrychis viciaefolia* Scop. cv. Nova) established in 1993. Sainfoin, rather than alfalfa, was used as a forage because the only available canola seeding area was located near the sainfoin. The sainfoin crop was divided into 3 stands (6.5 m x 87 m, 6.5 m x 87 m, 6.5 x 53 m) each of which was surrounded by a 5 m plant-free boundary.

Lygus Collections

Sweep-net collections were performed using a 38 cm (dia.) net. Sweeps were made in 180° arcs through the crop. Initially, sweeps were concentrated on the entire plant but later when plants were larger, only the top part of the canopy was swept. Sweeping was performed between 10:30-13:00 hours. In most cases, 100-sweeps were taken in a W-pattern over each stand of the canola and over the forage field. The W-

pattern was shifted randomly on successive sampling dates in both crops. In 1994, low insect numbers were obtained using the 100-sweep sampling method. Therefore, larger samples sizes were obtained by doing an additional sweep-net collection over the entire canola stand.

In 1994 and 1995, the growth stage of canola was calculated from 15 plants randomly sampled in a W-pattern over each stand (Harper and Berkenkamp 1975). In 1994, sweep-net collections began in the canola when it reached the rosette growth stage (2.6) on 27 June and continued every second day, weather permitting, until the early seeded canola stand reached the late flower stage of development (4.1) on 08 July. Sweep-net collections began in the late seeded canola stand at the rosette stage of development (2.3) on 08 July and continued every second day, weather permitting, until the early flower stage of development (4.2) on 27 July. Sweep-net collections were made weekly in the forage crop from 29 June - 14 July, 1994. In 1995, collections began in the early seeded stand of the canola on (2.1) on 11 May and continued every second day, weather permitting, until the early seeded canola stand reached the late flower stage of development (4.3) on 11 July. Collections began in the late seeded canola stand at the rosette stage of development (2.3) on 07 July and continued every second day, weather permitting, until the early flower stage of development (4.3) on 04 August. Sweep-net collections were made weekly in the forage crop from 15 June - 23 August, 1995.

Lygus collected by sweep-net were killed by immersion in a dissecting solution of glacial acetic acid, formaldehyde, and chloral hydrate (Weaver and Thomas 1956) which also preserved specimens. The species of *Lygus* collected were identified (Kelton

1983) and the ratio of males to females for each species was determined.

Lygus Dissections

To determine mating status and egg development status, female dissections were performed on preserved specimens as described in Section 3.3.1.

The relative size of the seminal depository was determined for *L. elisus* and *L. borealis* field collected females. The relative size of the seminal depository or the sperm receptacle organ of *Lygus* spp. (Davis 1955) was determined by assigning relative sizes to the observed seminal depository. Four relative sizes of the seminal depository were used to determine the mating status of the *Lygus* females collected (Section 3.3):

(1) Uninflated - the seminal depository is an uninflated, translucent, small membranous sac (0-10% of the size of an inflated seminal depository).
(2) Inflated - the seminal depository is an expanded, opaque, bulbous, greatly enlarged membranous sac.
(3) Partly Deflated - the seminal depository is an inflated, opaque, bulbous, large membranous sac (50-80% of the size of an inflated seminal depository).
(4) Deflated - the seminal depository is an uninflated, translucent, flattened, large membranous sac (10-30% of the size of an inflated seminal depository).

In 1994, stages 1, 3 and 4 were used to determine mating status. In 1995, the category, inflated, was added to describe the difference in size of the seminal depository thought to distinguish females that had mated immediately prior to collection.

Egg development status was based on the size, and the development of the oocytes contained within the ovarioles. *Lygus elisus* and *L. borealis* egg development

was separated into five categories:

(1) Non-reproductive - Right and left sets of ovarioles are reduced and transparent. Assumed to be either a newly eclosed or non-reproductive female.

(2) Previtellogenic - In both the right and left sets of ovarioles, oocytes are located in the extreme anterior ends of the transparent ovarioles. Oocytes appear as white masses rather than distinct units within the ovarioles. The ovarioles are reduced except at the anterior ends where the previtellogenic oocytes are housed (Fig. 4).

(3) Vitellogenic - Oocytes with yolk occupy the length of the ovarioles. These oocytes are white and individually visible within the ovarioles which are distended to contain the large sized oocytes (Fig. 5).

(4) Chorionated - Shiny, white oocytes are located posterior to vitellogenic oocytes in the ovarioles and in the common lateral oviducts. Chorionated oocytes are white and shiny and are individually visible within the distended ovarioles. Chorionated tanned caps of the oocytes are discernable through the ovarioles (Fig. 6).

(5) Post-oviposition - Small, white aggregations are visible in the extreme anterior ends of the distended, transparent ovarioles. No other oocytes visible within the ovarioles. Suspected to be oldest reproductively developed female.

Statistics

Collection periods corresponding to the period of time that a canola stand was at the modal rosette, bud, or flower crop stage (Harper and Berkenkamp 1975) were used to compare the *Lygus* collected in the canola. These same collection periods were used to separate the forage data. The null hypothesis was that mating status and patterns of reproductive development would be similar in the two crops at each canola growth stage.

Sweep-net collections began and ended in the early seeded stand of canola then began in the late seeded stand of canola in 1994. Therefore, sweep-net collections

followed chronological ordered periods from early to late seeded stands of canola in 1994. However, in 1995, sweep-net collections were performed simultaneously for a short period in both the early and late seeded stands of canola. Because the independent variable was canola crop stage rather than day of collection, sweep-net collections were grouped by the canola modal growth stage as in 1994. This resulted in some overlap in sweep-net collection periods between early and late seeded stands of canola in 1995 but the crop stage variable was maintained for comparison between years.

Chi-square (χ^2) tests (SAS Institute Inc. 1985; 1990) were used to test if both *L. elisus* and *L. borealis* sex ratios deviated from 1:1 in early and late seeded canola stands and one forage stand within each of the rosette, bud, and early flower sampling periods for 1994 and 1995 field data. Using main effects of crop and sampling periods corresponding to canola growth stages in categorical modelling (SAS Institute Inc. 1985; 1990), sex ratios were compared between the canola and forage crops separately for *L. elisus* and *L. borealis*. Using main effects of *Lygus* species and sampling periods corresponding to canola growth stages in categorical modelling (SAS Institute Inc. 1985; 1990), sex ratios were compared between *L. elisus* and *L. borealis* collections made separately in canola and forage crop. For the above three categorical models interactions were examined using a nested-by-effect model statement in categorical modelling where effect was rosette, bud, or flower sampling periods. In all sex ratio comparisons, 1994 and 1995 data were analysed independently. In 1994, sweep-net collections were performed in the forage at stages corresponding to only the early bud, early flower, and late rosette stages of canola. Therefore, to prevent impossible comparisons of unbalanced

data sets, the 1994 categorical modelling compared between canola and forage only when stages were available for both crops. Comparisons of *L. elisus* and *L. borealis* in the canola included early rosette, early bud, early flower, late rosette, late bud, and late flower sampling periods. Comparisons of *L. elisus* and *L. borealis* in forage included only early bud, early flower, and late rosette sampling periods.

The above analyses were repeated to examine female mating status, and female egg development frequencies.

4.4 Results

Results from categorical modelling comparing *L. elisus* sex ratios between canola and forage crops, *L. borealis* sex ratios between canola and forage crops, or between *L. elisus* and *L. borealis* in canola, and between *L. elisus* and *L. borealis* in forage crops involved the comparison of sample sizes that varied considerably between sampling periods. Sample sizes forming the row or column means in the contingency table constructed by the categorical modeling varied for both species of *Lygus* compared and in both crops in 1994 and 1995 (Fig. 21, 22, 23). This relative difference in sample sizes compared affects main effects, biasing results towards the relatively larger sample sizes which form row totals used in the categorical modeling. The discrepancy between sample sizes compared was partly due to the difficulty in sampling insects early in the season (e.g., rosette sampling period) but also due to the effect of grouping data by sampling periods which were related to canola crops stage in all categorical modelling comparisons.

Figure 21. Proportion of *Lygus* species males (■) to females (□) collected by sweep-net from early and late seeded canola and a forage stand. Sweep-net collections were performed during sampling periods defined as the days elapsed when the early and late seeded stands of canola were at the rosette, bud, and early flower crop development stages in each year. A. *Lygus elisus* (Van Duzee) collected in canola (**C**) and alfalfa (**F**) in 1994; B. *Lygus elisus* (Van Duzee) collected in canola (**C**) and sainfoin (**F**) in 1995; C. *Lygus borealis* (Kelton) collected in canola (**C**) and alfalfa (**F**) in 1994; D. *Lygus borealis* (Kelton) collected in canola (**C**) and sainfoin (**F**) in 1995. Numbers above each bar indicate the sample size for each collection period. Asterisks indicate significant deviation from 1:1 sex ratio determined by Chi-square test ($P<0.05$, $df=1$). Refer to Table 3 for *L. elisus* and Table 6 for *L. borealis* statistics.

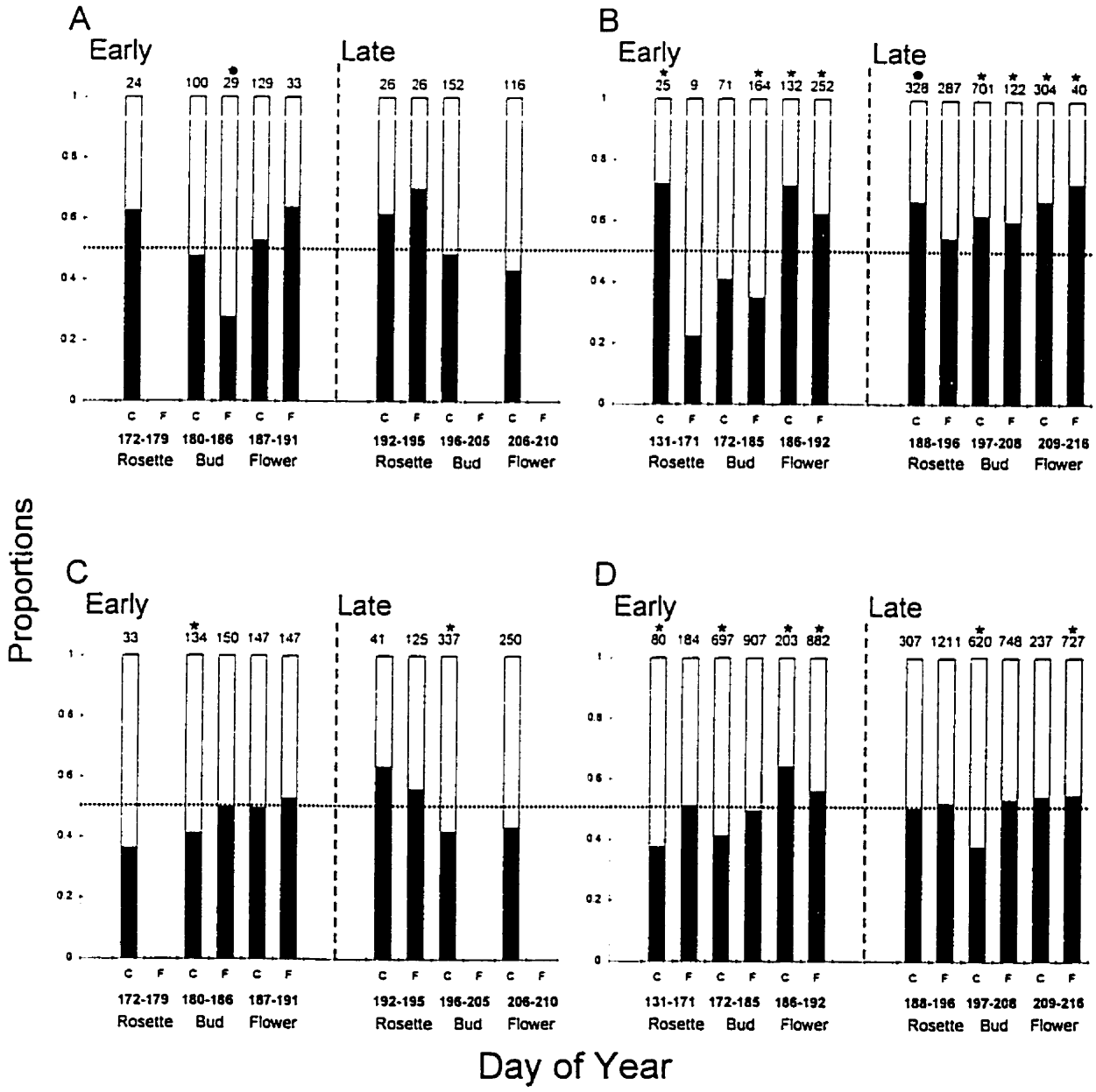
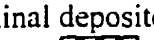
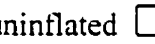

A
Early
Late
24 100 29 129 33
26 26 152 116
B
Early
Late
25 9 71 164 132 252
328 287 701 122 304 40
C
Early
Late
33 134 150 147 147
41 125 337 250
D
Early
Late
80 184 697 907 203 882
307 1211 620 748 237 727
C F C F C F
172-179 Rosette
180-186 Bud
187-191 Flower
192-195 Rosette
196-205 Bud
206-210 Flower
131-171 Rosette
172-185 Bud
186-192 Flower
188-196 Rosette
197-208 Bud
209-216 Flower
Proportions
Day of Year

Figure 22. Proportion of *Lygus* species females at various mating status stages, determined by the relative size of the seminal depository (uninflated  , deflated  , partly deflated  , inflated ), collected by sweep-net from early and late seeded canola and a forage stand in 1994 and 1995. Sweep-net collections were performed during sampling periods defined as the days elapsed when the early and late seeded stands of canola were at the rosette, bud, and early flower crop development stages in each year. A. *Lygus elisus* (Van Duzee) collected in canola (**C**) and alfalfa (**F**) in 1994; B. *Lygus elisus* (Van Duzee) collected in canola (**C**) and sainfoin (**F**) in 1995; C. *Lygus borealis* (Kelton) collected in canola (**C**) and alfalfa (**F**) in 1994; D. *Lygus borealis* (Kelton) collected in canola (**C**) and sainfoin (**F**) in 1995. Numbers above each bar indicate the sample size for each collection period.

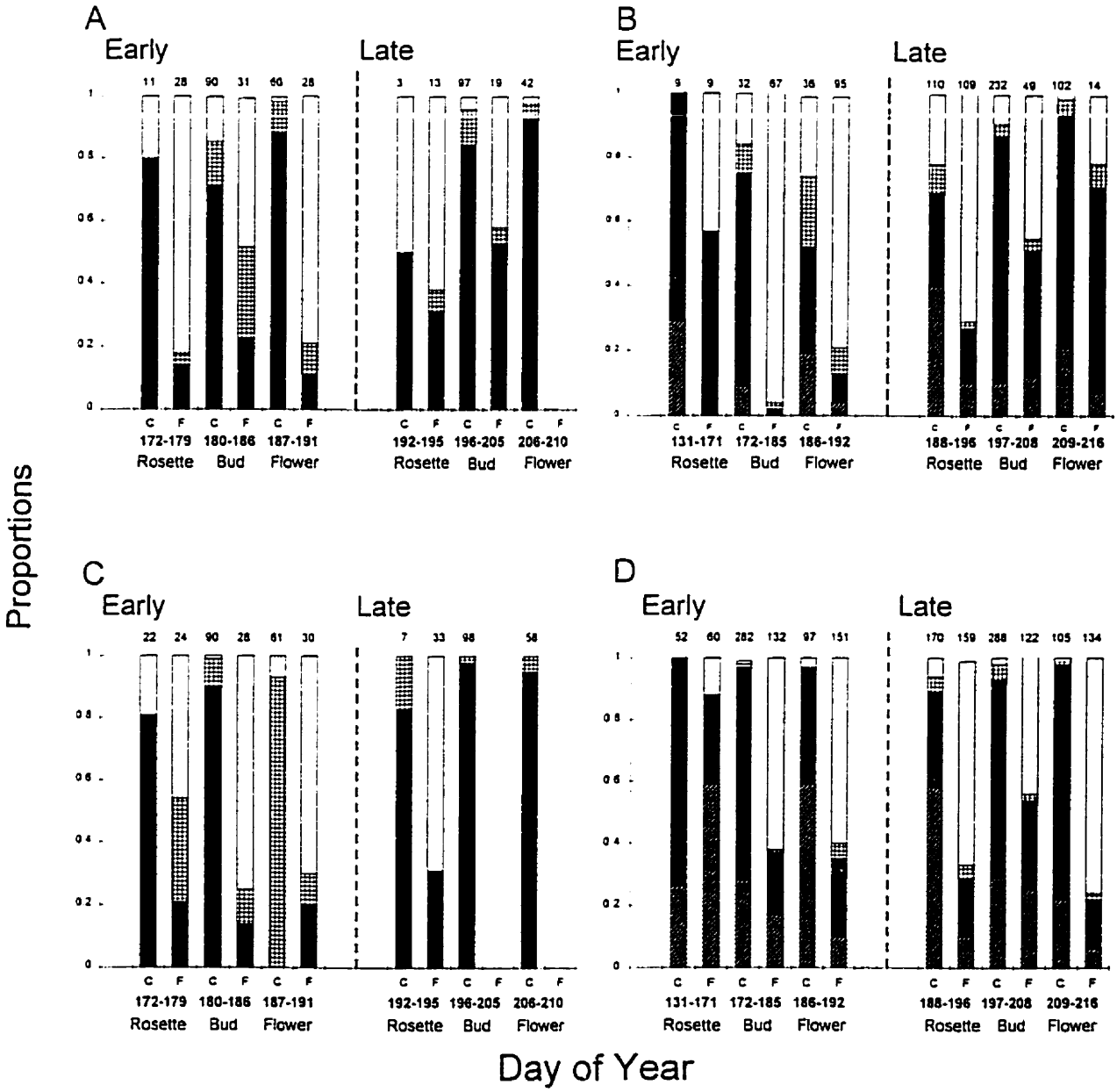
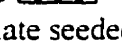
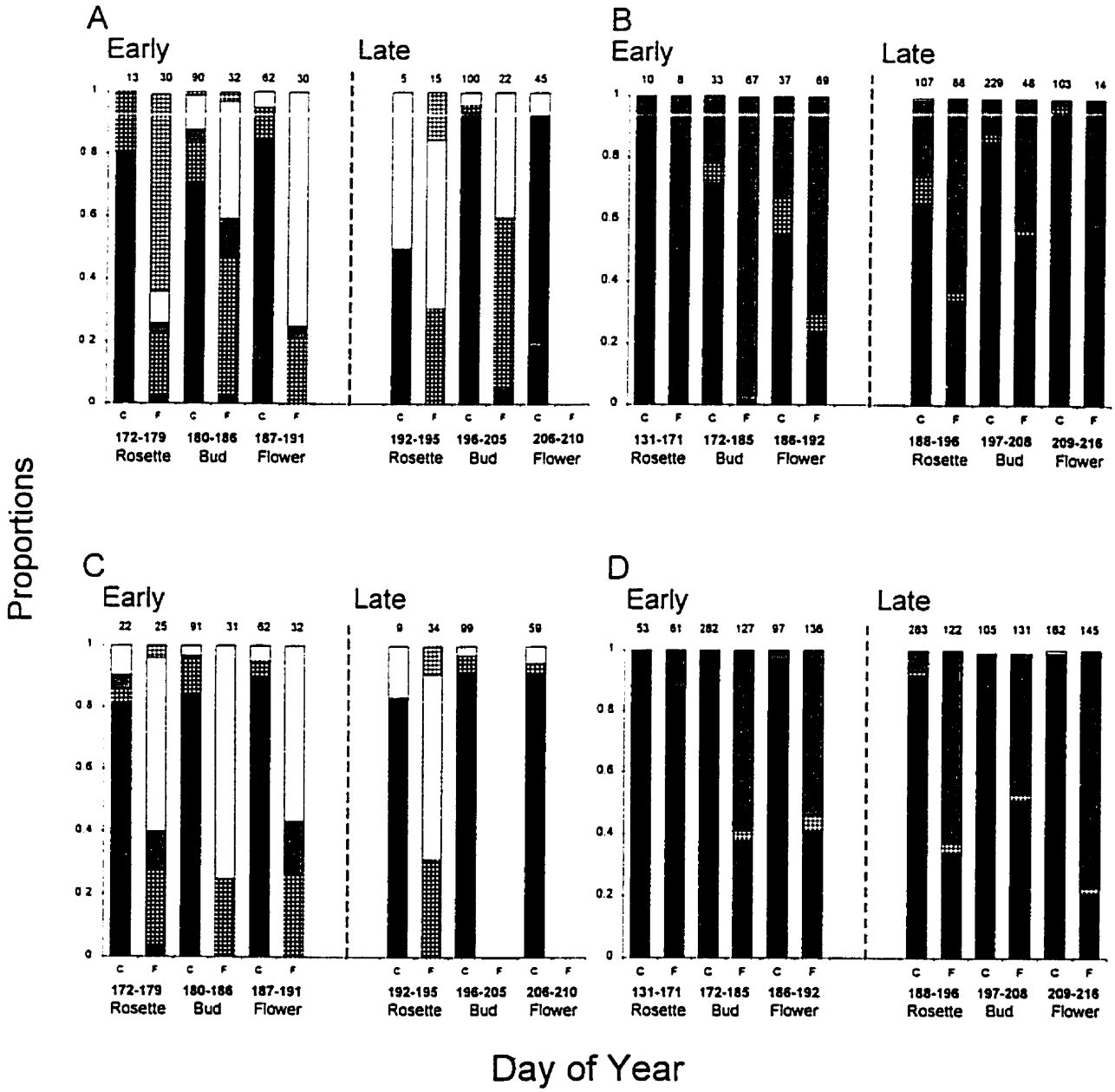

A
Early
Late
11 28 90 31 60 28
3 13 97 19 42
C F C F C F
172-179 180-186 187-191
Rosette Bud Flower
C F C F C F
192-195 196-205 206-210
Rosette Bud Flower
B
Early
Late
9 9 32 67 36 95
110 109 232 49 102 14
131-171 172-185 186-192
Rosette Bud Flower
188-196 197-208 209-216
Rosette Bud Flower
C
Early
Late
22 24 90 28 61 30
7 33 98 58
172-179 180-186 187-191
Rosette Bud Flower
192-195 196-205 206-210
Rosette Bud Flower
D
Early
Late
52 60 282 132 97 151
170 159 288 122 105 134
131-171 172-185 186-192
Rosette Bud Flower
188-196 197-208 209-216
Rosette Bud Flower
Proportions
Day of Year

Figure 23. Proportion of *Lygus* species females at various egg development stages, determined by oocyte stages within ovarioles (non-reproductive  , post-ovipositional  , previtellogenic  , vitellogenic  or chorionated ), collected by sweep-net from early and late seeded canola and a forage stand in 1994 and 1995. Sweep-net collections were performed during sampling periods defined as the days elapsed when the early and late seeded stands of canola were at the rosette, bud, and early flower crop development stages in each year. A. *Lygus elisus* (Van Duzee) collected in canola (**C**) and alfalfa (**F**) in 1994; B. *Lygus elisus* (Van Duzee) collected in canola (**C**) and sainfoin (**F**) in 1995; C. *Lygus borealis* (Kelton) collected in canola (**C**) and alfalfa (**F**) in 1994; D. *Lygus borealis* (Kelton) collected in canola (**C**) and sainfoin (**F**) in 1995. Numbers above each bar indicate the sample size for each collection period.


A
Early
Late
B
Early
Late
C
Early
Late
D
Early
Late
Proportions
Day of Year
172-179 Rosette
180-186 Bud
187-191 Flower
192-195 Rosette
196-205 Bud
206-210 Flower
131-171 Rosette
172-185 Bud
186-192 Flower
188-196 Rosette
197-208 Bud
209-216 Flower

4.4.1 Sex Ratio Results

Lygus elisus. In 1994, the *L. elisus* sex ratio did not significantly deviate from a 1:1 ratio during the rosette, bud, or flower sampling periods in either the early or late seeded stands of canola (Table 3). Similarly in forages, *L. elisus* sex ratios did not deviate significantly from a 1:1 ratio in 1994 except during the early-seeded bud sampling period when there was a low frequency of males (Table 3) (Fig. 21 A). In 1995, significantly fewer males were present in the canola which changed to significantly more males during the early-seeded flower sampling periods (Table 3) (Fig. 21 B). Significantly fewer males were present in the canola in 1995 during the early-seeded bud sampling period, however, significantly more males than females were present during the early-seeded flower and again in the late-seeded bud and flower sampling periods (Table 3) (Fig. 21 B).

Comparison of *L. elisus* Collected in Canola and Forage Crops. When comparing sex ratios between the canola and forage crops for *L. elisus* using main effects of crop and sampling periods corresponding to canola growth stages in categorical modelling, sample sizes forming the row or column means in the contingency table varied from 26 to 152 in 1994 (Fig. 21 A), 9 to 252 in early 1995, and 40 to 701 in late 1995 comparisons (Fig. 21 B).

In 1994, *L. elisus* sex ratios did not significantly differ between the canola and forage crops (Table 4) (Fig. 21 A). There was a significant difference in sex ratios during the sampling periods (Table 4) (Fig. 21 A) with increasingly more males from the early-seeded bud (mean ±SE, 0.38±0.10), early-seeded flower (0.58±0.13), to late-seeded

Table 3: Comparison[1] of *Lygus elisus* male to female proportions for each sampling period in each crop from individuals collected by sweep-net in canola and forage crops in 1994 and 1995.

		1994		1995	
		Canola[2]	Forage[3]	Canola[4]	Forage[5]
Early-Seeded Sampling Periods	Rosette	$\chi^2 = 1.50$ P= 0.2207 df= 1		$\chi^2 = 4.84$ **P= 0.0278** df= 1	$\chi^2 = 2.78$ P= 0.0956 df= 1
	Bud	$\chi^2 = 0.36$ P= 0.5485 df= 1	$\chi^2 = 5.83$ **P= 0.0158** df= 1	$\chi^2 = 2.38$ P= 0.1229 df= 1	$\chi^2 = 15.24$ **P< 0.0001** df= 1
	Flower	$\chi^2 = 0.38$ P= 0.5377 df= 1	$\chi^2 = 2.45$ P= 0.1172 df= 1	$\chi^2 = 25.48$ **P< 0.0001** df= 1	$\chi^2 = 15.25$ **P< 0.0001** df= 1
Late-Seeded Sampling Periods	Rosette	$\chi^2 = 1.38$ P= 0.2393 df= 1	$\chi^2 = 3.20$ P= 0.0736 df= 1	$\chi^2 = 35.56$ **P< 0.0001** df= 1	$\chi^2 = 2.18$ P= 0.1400 df= 1
	Bud	$\chi^2 = 0.11$ P= 0.7456 df= 1		$\chi^2 = 39.78$ **P< 0.0001** df= 1	$\chi^2 = 4.72$ **P= 0.0298** df= 1
	Flower	$\chi^2 = 2.21$ P= 0.1374 df= 1		$\chi^2 = 34.22$ **P< 0.0001** df= 1	$\chi^2 = 8.10$ **P= 0.0044** df= 1

[1] 1 x 2 Chi-square (χ^2)Test (SAS Institute Inc. 1985; 1990) testing deviation from a 1:1 male:female sex ratio
[2] *Brassica napus* cv. Legend
[3] *Medicago sativa* L.
[4] *B. napus* cv. Westar
[5] *Onobrychis viciaefolia* Scop. cv. Nova

Table 4: Comparison[1] of sex ratios between canola and forage crops and between sampling periods for both *Lygus elisus* and *L. borealis* collected by sweep-net in 1994 and 1995.

	Lygus elisus			*Lygus borealis*		
	χ^2	P	df	χ^2	P	df
1994						
Intercept	278.77	**<0.0001**	1	724.56	**<0.0001**	1
Crops[2]	0.06	0.80	1	0.95	0.33	1
Sampling Periods [3]	10.00	**0.01**	2	5.61	0.06	2
Crops x Sampling Periods	5.65	0.06	2	2.42	0.30	2
1995 Early						
Intercept	357.33	**<0.0001**	1	1545.72	**<0.0001**	1
Crops[4]	7.57	**0.01**	1	4.74	**0.03**	1
Sampling Periods	51.62	**<0.0001**	2	29.92	**<0.0001**	2
Crops x Sampling Periods	6.09	**0.05**	2	15.61	**<0.0001**	2
1995 Late						
Intercept	1913.43	**<0.0001**	1	3063.29	**<0.0001**	1
Crops[4]	4.77	**0.03**	1	18.48	**<0.0001**	1
Sampling Periods	3.65	0.16	2	10.81	**<0.0001**	2
Crops x Sampling Periods	5.49	0.06	2	15.61	**<0.0001**	2

[1] PROC CATMOD (SAS Institute Inc. 1985; 1990) using main effects (crops and sampling period)
[2] *Brassica napus* cv. Legend and *Medicago sativa* L.
[3] Sampling periods compared in 1994 correspond to days 180-186, 187-191, and 192-195 which avoided comparisons with unbalanced data.
[4] *B. napus* cv. Westar and *Onobrychis viciaefolia* Scop. cv. Nova

rosette (0.66±0.04) periods. There was no significant interaction between the crops and sampling periods compared (Table 4).

In early-seeded sampling in 1995, significantly more males were observed in the canola (0.61±0.08) relative to forage (0.40±0.10) (Table 4) (Fig. 21 B). There was a significant difference in sex ratios observed between the canola and forage crops during the rosette and flower periods (Table 5) and there was a significant interaction between crops and early sampling periods compared (Table 4). The frequency of males decreased from the rosette (0.72), to bud (0.41) then increased in the flower (0.72) sampling period in the canola whereas the ratio of males increased throughout the corresponding sampling periods in the forage 0.22 at rosette,0.35 at bud, and 0.62 at flower) (Table 4) (Fig. 21 B).

In late-seeded sampling in 1995, there was a significant difference in *L. elisus* sex ratios between the canola and forage crops in 1995 (Table 4) (Fig. 21 B). Higher frequencies of *L. elisus* males were present in the canola (0.61±0.08) than in forage (0.40±0.10). There was no significant difference in the sex ratios observed during late-seeded sampling periods and there was no significant interaction between the crops and sampling periods compared (Table 4).

Lygus borealis. In 1994, *L. borealis* sex ratios did not significantly deviate from a 1:1 ratio in the canola except during early-seeded bud and late-seeded bud sampling periods (Table 6) when there were significantly more females than males (Fig. 21 C). *Lygus borealis* sex ratios did not deviate from a 1:1 ratio in forage in 1994 (Table 6) (Fig. 21 C). In 1995, sex ratios fluctuated in the canola (Table 6) beginning with significantly fewer males in the early-seeded rosette, and bud, then increasing in the early-seeded

Table 5: Comparison[1] of sex ratios between canola and forage crops and between sampling periods for both *Lygus elisus* and *L. borealis* collected by sweep-net in 1994 and 1995.

	Lygus elisus			*Lygus borealis*		
	χ^2	P	df	χ^2	P	df
1995 Early						
Intercept	267.93	**<0.0001**	1	1421.85	**<0.0001**	1
Crops[2]						
(Rosette)	9.09	**0.003**	1	4.66	**0.03**	1
(Bud)	0.77	0.38	1	11.13	**0.0008**	1
(Flower)	3.80	**0.05**	1	4.56	**0.03**	1
Sampling Periods	48.91	**<0.0001**	2	44.69	**<0.0001**	2
Crops x Sampling Periods	.	.	0	.	.	0
1995 Late						
Intercept				2910.38	**<0.0001**	1
Crops[3]						
(Rosette)				0.31	0.58	1
(Bud)				33.75	**<0.0001**	1
(Flower)				0.03	0.87	1
Sampling Periods				17.29	**<0.0001**	2
Crops x Sampling Periods				.	.	0

[1] PROC CATMOD (SAS Institute Inc. 1985; 1990) using nested-by-effects (sampling period)
[2] *Brassica napus* cv. Legend and *Medicago sativa* L.
[3] *B. napus* cv. Westar and *Onobrychis viciaefolia* Scop. cv. Nova

Table 6: Comparison[1] of *Lygus borealis* male to female proportions for each sampling period in each crop from individuals collected by sweep-net in canola and forage crops in 1994 and 1995.

		1994		1995	
		Canola[2]	Forage[3]	Canola[4]	Forage[5]
Early-Seeded Sampling Periods	Rosette	$\chi^2 = 2.45$ P= 0.1172 df= 1		$\chi^2 = 5.00$ **P= 0.0253** df= 1	$\chi^2 = 0.20$ P= 0.6583 df= 1
	Bud	$\chi^2 = 4.30$ **P= 0.0382** df= 1	$\chi^2 < 0.0001$ P= 1.0000 df= 1	$\chi^2 = 21.71$ **P< 0.0001** df= 1	$\chi^2 = 0.09$ P= 0.7651 df= 1
	Flower	$\chi^2 = 0.01$ P= 0.9343 df= 1	$\chi^2 = 0.55$ P= 0.4579 df= 1	$\chi^2 = 16.00$ **P< 0.0001** df= 1	$\chi^2 = 12.74$ **P= 0.0004** df= 1
Late-Seeded Sampling Periods	Rosette	$\chi^2 = 2.95$ P= 0.0858 df= 1	$\chi^2 = 1.80$ P= 0.1797 df= 1	$\chi^2 = 0.003$ P= 0.9545 df= 1	$\chi^2 = 1.82$ P= 0.1768 df= 1
	Bud	$\chi^2 = 10.33$ **P= 0.0013** df= 1		$\chi^2 = 38.25$ **P< 0.0001** df= 1	$\chi^2 = 2.83$ P= 0.0926 df= 1
	Flower	$\chi^2 = 3.60$ P= 0.0578 df= 1		$\chi^2 = 1.52$ P= 0.2171 df= 1	$\chi^2 = 6.17$ **P= 0.0130** df= 1

[1] 1 x 2 Chi-square (χ^2)Test (SAS Institute Inc. 1985; 1990) testing deviation from a 1:1 male:female sex ratio
[2] *Brassica napus* cv. Legend
[3] *Medicago sativa* L.
[4] *B. napus* cv. Westar
[5] *Onobrychis viciaefolia* Scop. cv. Nova

flower sampling period (Fig. 21 D). By the late-seeded bud sampling period, the frequency of males decreased in the canola (Fig. 21 D). High frequencies of males were present in forage in 1995 during early-seeded flower and late-seeded flower sampling periods (Fig. 21 D).

Comparison of *L. borealis* Collected in Canola and Forage Crops. In the comparison of sex ratios between the canola and forage crops for *L. borealis* using main effects of crop and sampling periods corresponding to canola growth stages in categorical modelling, sample sizes forming the row or column means in the contingency table varied from 41 to 151 in 1994 (Fig. 21 C), 80 to 907 in early 1995, and 237 to 1211 in late 1995 comparisons (Fig. 21 D).

In 1994 there was no significant difference in *L. borealis* sex ratios observed in the canola and forage crops (Table 4) (Fig. 21 C). There was no significant difference between the sex ratios during the sampling periods compared and there was no significant interaction between the crops and sampling periods (Table 4) (Fig. 21 C).

In early-seeded sampling in 1995, *L. borealis* sex ratios observed in the canola and forage crops were significantly different (Table 4) (Fig. 21 D). Male frequencies significantly increased between the early sampling periods (Table 4) (Fig. 21 D) from the rosette (0.44±0.07), bud (0.45±0.04), to flower (0.60±0.04). There was a significant interaction between crops and sampling periods (Table 4) (Fig. 21 D) related to a significant difference in sex ratios between canola and forage crops at the rosette, bud, and flower sampling periods (Table 5). Male frequencies increased from 0.38 to 0.41 to 0.64 in the canola during the rosette, bud and flower sampling periods whereas the

frequency of males decreased slightly from the corresponding rosette (0.51) to the bud sampling periods (0.50) then increased slightly at the flower (0.56) period in the forage crop (Fig. 21 D).

In late 1995, there was a significant difference in *L. borealis* sex ratios between the crops (Table 4) (Fig. 21 D) with lower frequencies of males in the canola (0.47±0.04) than in forage (0.53±0.01). There was a significant difference in sex ratios observed between the late sampling periods (Table 4) (Fig. 21 D) with fluctuations between the rosette (0.51±0.01), bud (0.45±0.08), and flower (0.54±0.003) periods. There was a significant interaction between sex ratios and sampling periods (Table 4) caused by a significant difference in sex ratios in the canola and forage crops in the bud sampling period (Table 5). Frequencies of males remained relatively constant during the rosette, bud, and flower sampling periods in the forage ranging between 0.52 to 0.55 while in the canola, male frequencies decreased from 0.50 (rosette) to 0.38 (bud) then increased to 0.54 (flower) during the corresponding sampling periods (Fig. 21 D).

Comparison of *Lygus* species Collected in Canola. The sample sizes forming the row or column means in the contingency table varied from 24 to 337 in 1994 (Fig. 21 A & C), 25 to 697 in early 1995, and 237 to 701 in late 1995 comparisons (Fig. 21 B & D) when comparing sex ratios between the *L. elisus* and *L. borealis* collected in canola using main effects of *Lygus* species and sampling periods corresponding to canola growth stages in categorical modelling.

In 1994, there was no difference in sex ratios between *L. elisus* and *L. borealis* collected in the canola (Table 7) (Fig. 21 A & C). There was a significant difference in

Table 7: Comparison[1] of sex ratios between *Lygus elisus* and *L. borealis* species collected by sweep-net and between sampling periods in both canola and forage crops in 1994 and 1995.

	Canola			Forage		
	χ^2	P	df	χ^2	P	df
1994[2]						
Intercept	788.92	**<0.0001**	1	343.60	**<0.0001**	1
species	3.07	0.08	1	0.03	0.87	1
Sampling Periods[3]	12.52	**0.03**	5	5.95	**0.05**	2
species x Sampling Periods	4.47	0.48	5	8.70	**0.01**	2
1995 Early[4]						
Intercept	681.07	**<0.0001**	1	929.29	**<0.0001**	1
species	4.96	**0.03**	1	1.78	0.18	1
Sampling Periods	50.26	**<0.0001**	2	25.93	**<0.0001**	2
species x Sampling Periods	8.2	**<0.0001**	2	18.81	**<0.0001**	2
1995 Late[4]						
Intercept	2846.99	**<0.0001**	1	1830.63	**<0.0001**	1
species	103.31	**<0.0001**	1	4.70	**0.03**	1
Sampling Periods	21.86	**<0.0001**	2	3.38	0.18	2
species x Sampling Periods	6.47	**0.04**	2	3.84	0.15	2

[1] PROC CATMOD (SAS Institute Inc. 1985; 1990) using main effects (species and sampling period)

[2] *Brassica napus* cv. Legend and *Medicago sativa* L.

[3] Sampling periods in 1994 in canola correspond to days 172-179, 180-186, 187-191, 192-195, 196-205 and 206-210 but in forage, only days 180-186, 187-191, and 192-195 were compared which avoided unbalanced data sets.

[4] *B. napus* cv. Westar and *Onobrychis viciaefolia* Scop. cv. Nova

the sex ratios between the sampling periods (Table 7) (Fig. 21 A & C) with a decrease in the frequency of males from early rosette (0.49±0.13) to early bud (0.21±0.03) which increased at late rosette (0.62±0.01) then decreased by late flower sampling period (0.43±0.002). There was no significant interaction between species and sampling periods compared (Table 7).

In 1995, there was a significant difference in sex ratios between *L. elisus* (0.61±0.08) and *L. borealis* (0.48±0.07) individuals collected in the early canola (Table 7) (Fig. 21 B & D). Male frequencies significantly fluctuated between early rosette (0.55±0.17), bud (0.41±0.002), and flower (0.68±0.04) sampling periods (Table 7) (Fig. 21 B & D). There was a significant interaction between species and sampling periods caused by a significant difference in the sex ratios during the rosette sampling period and across sampling periods compared (Table 8). At the rosette period, *L. elisus* male frequencies were significantly higher (0.72) than *L. borealis* (0.38). *Lygus elisus* male frequencies then decreased from the rosette (0.72) to bud (0.41) but increased at flower (0.72) whereas *L. borealis* male frequencies were low at the rosette stage (0.38) and increased during the corresponding sampling periods (0.41 at bud to 0.64 at flower) (Fig. 21 B & D, Early).

There was a significant difference in the sex ratios between *L. elisus* (0.65±0.01) and *L. borealis* (0.47±0.04) in the late 1995 canola (Table 7) (Fig. 21 B & D). As in the early canola, male frequencies were significantly different between the sampling periods decreasing from the late rosette (0.58±0.08) to the bud (0.50±0.12) then increasing by the flower (0.60±0.06) sampling period (Table 7) (Fig. 21 B & D). There was a significant

Table 8: Comparison[1] of sex ratios between *Lygus elisus* and *L. borealis* species collected by sweep-net and between sampling periods in both canola and forage crops in 1994 and 1995.

	Canola			Forage		
	χ^2	P	df	χ^2	P	df
1994[2]						
Intercept				345.01	**<0.0001**	1
species						
(Early Bud)				5.87	**0.02**	1
(Early Flower)				1.28	0.26	1
(Late Rosette)				1.57	0.21	1
Sampling Periods[3]				13.88	**0.001**	2
species x Sampling Periods				.	.	0
1995 Early[4]						
Intercept	616.28	**<0.0001**	1	326.10	**<0.0001**	1
species						
(Rosette)	10.83	**0.001**	1	4.21	**0.04**	1
(Bud)	0.00	0.96	1	13.12	**0.0003**	1
(Flower)	2.36	0.12	1	3.27	0.07	1
Sampling Periods	45.58	**<0.0001**	2	44.66	**<0.0001**	2
species x Sampling Periods	.	.	0	.	.	0
1995 Late[4]						
Intercept	2847.21	**<0.0001**	1			
species						
(Rosette)	17.79	**<0.0001**	1			
(Bud)	82.83	**<0.0001**	1			
(Flower)	9.17	**0.003**	1			
Sampling Periods	24.26	**<0.0001**	2			
species x Sampling Periods	.	.	0			

[1] PROC CATMOD (SAS Institute Inc. 1985; 1990) using nested-by-effects (sampling periods)
[2] *Brassica napus* cv. Legend and *Medicago sativa* L.
[3] Sampling periods in 1994 in canola correspond to days 172-179, 180-186, 187-191, 192-195, 196-205 and 206-210 but in alfalfa, only days 180-186, 187-191, and 192-195 were compared which avoided unbalanced data sets.
[4] *B. napus* cv. Westar and *Onobrychis viciaefolia* Scop. cv. Nova

interaction between *Lygus* species compared and late sampling periods caused by a significant difference in sex ratios between species which occurred at the late rosette, bud, and flower sampling periods (Table 8). Although male frequencies followed the same general pattern of decreasing at the bud sampling period relative to the rosette and flower periods, *L. elisus* male frequencies were significantly higher than *L. borealis* at all three sampling periods (Fig. 21 B & D, Late).

Comparison of *Lygus* species Collected in Forages. The sample sizes forming the row or column means in the contingency table varied from 26 to 150 in 1994 (Fig. 21A & C), 9 to 907 in early 1995, and 40 to 1211 in late 1995 comparisons (Fig. 21 B & D) when comparing sex ratios between the *L. elisus* and *L. borealis* collected in forage crops using main effects of *Lygus* species and sampling periods corresponding to canola growth stages in categorical modelling.

There was no significant difference in the sex ratios observed for *L. elisus* and *L. borealis* in the 1994 forage (Table 7) (Fig. 21 A & C). However, there was a significant difference in sex ratios observed between the sampling periods (Table 7) (Fig. 21 A & C) with an increase in male frequencies from the early-seeded bud (0.25±0.11), early-seeded flower (0.58±0.05) to late-seeded rosette (0.63±0.07). There was a significant interaction effect between *Lygus* species and sampling periods related to significant differences in sex ratios between *L. elisus* and *L. borealis* at the early bud sampling period (Table 8). Significantly lower frequencies of male *L. elisus* (0.28) than *L. borealis* (0.50) were present in the canola during the early bud sampling period (Table 8). *Lygus elisus* male frequencies increased from the early-seeded bud (0.28) to the early-seeded flower periods

(0.64) and increased again by the late-seeded rosette period (0.70). *Lygus borealis* followed a similar pattern with male frequencies increasing from the early-seeded bud (0.50) to early-seeded flower (0.53) and slightly increasing again at the late-seeded rosette period (0.56) (Fig. 21 A & C).

In early 1995, there was no significant difference in sex ratios between *L. elisus* (0.40±0.10) and *L. borealis* (0.52±0.02) collected in forage (Table 7) (Fig. 21 B & D). There was a significant difference in sex ratios between the early sampling periods with male frequencies increasing from the rosette (0.53±0.01), bud (0.56±0.03), to flower (0.64±0.09) sampling period (Table 7) (Fig. 21 B & D). There was a significant interaction between species and sampling periods caused by significant differences in sex ratios between *L. elisus* and *L. borealis* at the rosette and bud sampling periods (Table 8). *Lygus borealis* male frequencies were significantly higher than *L. elisus* in the forage during all three early sampling periods (Table 8). Low frequencies of *L. elisus* males were present during the rosette sampling period (0.22) but increased at the bud (0.35) and flower sampling periods (0.62). In contrast, relatively higher male frequencies of *L. borealis* were present at the rosette stage (0.51) which decreased at the bud stage (0.50) but increased again at the flower sampling period (0.56) (Fig. 21 B & D, Early).

In late 1995, there was a significant difference in sex ratios between *L. elisus* (0.38±0.04) and *L. borealis* (0.47±0.006) collected in forage (Table 7) (Fig. 21 B and D). There was no significant difference in sex ratios between the late sampling periods and there was no significant interaction between species and sampling periods (Table 7) (Fig. 21 B & D).

4.4.2 Female Mating Status Results

Comparison of *L. elisus* Collected in Canola and Forage Crops. When comparing mating status frequencies between the canola and forage crops for *L. elisus* using main effects of crop and sampling periods corresponding to canola growth stages in categorical modelling, sample sizes forming the row or column means in the contingency table varied from 3 to 97 in 1994 (Fig. 22 A), 9 to 95 in early 1995, and 14 to 232 in late 1995 comparisons (Fig. 22 B).

In 1994 and 1995, there was a significant difference between *L. elisus* in canola and forage (Table 9) where high frequencies of females had partly deflated seminal depositories in the canola and high frequencies of females had uninflated seminal depositories in the forage (Table 10) (Fig. 22 A & B). The frequencies of mated (females with inflated, partly deflated, or deflated seminal depositories) and unmated females (uninflated seminal depositories) accentuated the difference between crops where high numbers of *L. elisus* females were mated in the canola and low numbers were mated in the forage (Table 10). There was a significant difference in *L. elisus* mating status frequencies during the sampling periods in 1994, early-seeded 1995, and late-seeded 1995 (Table 9). *Lygus elisus* mating status frequencies changed over the sampling periods compared in both 1994 and 1995, and in the early and late sampling periods in 1995, although no consistent pattern could be discerned (Table 10) (Fig. 22 A & B). In 1994, high frequencies of females were unmated at the rosette sampling periods but by bud and flower sampling periods, higher frequencies of females had partly deflated seminal depositories (Table 10) (Fig. 22 A). This was not observed in 1995 and instead,

Table 9: Comparison[1] of female mating status ratios between canola and forage crops and between sampling periods for both *Lygus elisus* and *L. borealis* collected by sweep-net in 1994 and 1995.

	Lygus elisus			*Lygus borealis*		
	χ^2	P	df	χ^2	P	df
1994						
intercept	301.52	**<0.0001**	2	292.35	**<0.0001**	2
Crops[2]	176.49	**<0.0001**	2	221.20	**<0.0001**	2
Sampling Periods[3]	15.41	**0.05**	8	6.08	0.41	6
Crops x Sampling Periods	23.38	**0.003**	8	12.82	**0.05**	6
1995 Early						
Intercept	859.24	**<0.0001**	3	1555.65	**<0.0001**	3
Crops[4]	159.09	**<0.0001**	3	177.45	**<0.0001**	3
Sampling Periods	18.00	**0.01**	6	119.38	**<0.0001**	6
Crops x Sampling Periods	17.67	**0.01**	6	293.81	**<0.0001**	6
1995 Late						
Intercept	2914.08	**<0.0001**	3	4204.72	**<0.0001**	3
Crops[4]	84.96	**<0.0001**	3	675.81	**<0.0001**	3
Sampling Periods	117.17	**<0.0001**	6	39.54	**<0.0001**	6
Crops x Sampling Periods	27.88	**<0.0001**	6	85.23	**<0.0001**	6

[1] PROC CATMOD (SAS Institute Inc. 1985; 1990) using main effects (crops and sampling period)

[2] *Brassica napus* cv. Legend and *Medicago sativa* L.

[3] Sampling periods compared in 1994 for *L. elisus* correspond to days 172-179, 180-186, 187-191, 192-195, and 196-205 and for *L. borealis*, correspond to days 172-179, 180-186, 187-191, and 192-195 which avoided comparisons with unbalanced data.

[4] *B. napus* cv. Westar and *Onobrychis viciaefolia* Scop. cv. Nova

Table 10: Mean (±SE) female mating status frequencies for both *Lygus elisus* and *L. borealis* sweep-net collected in canola and forage crops during the early-seeded rosette, bud, flower and late-seeded rosette, bud, and flower sampling periods in 1994 and 1995.

	1994				1995			
	Partly Deflated	Deflated	Uninflated		Inflated	Partly Deflated	Deflated	Uninflated
Lygus elisus								
Crops *					**Early ***	**Late ***		
Canola	0.75±0.06	0.09±0.02	0.18±0.08	Early	0.19±0.05	0.57±0.10	0.10±0.05	0.14±0.06
				Late	0.24±0.07	0.60±0.13	0.06±0.01	0.11±0.05
Forage	0.26±0.07	0.11±0.04	0.63±0.07	Early	0.01±0.02	0.23±0.29	0.03±0.02	0.73±0.13
				Late	0.10±0.01	0.40±0.11	0.04±0.01	0.46±0.12
Sampling Periods *					**Early ***	**Late ***		
172-179	0.47±0.33	0.07±0.03	0.51±0.31	131-171	0.15±0.15	0.64±0.07	0.00±0.00	0.22±0.22
180-186	0.47±0.24	0.22±0.07	0.31±0.17	172-185	0.05±0.05	0.34±0.32	0.06±0.04	0.57±0.41
187-191	0.50±0.39	0.11±0.01	0.40±0.39	186-192	0.12±0.08	0.21±0.12	0.15±0.07	0.52±0.27
192-195	0.41±0.10	0.04±0.04	0.56±0.06	188-196	0.25±0.15	0.23±0.06	0.06±0.04	0.47±0.25
196-205	0.69±0.16	0.08±0.03	0.23±0.19	197-208	0.11±0.01	0.58±0.19	0.04±0.00	0.27±0.18
206-210	.	.	.	209-216	0.14±0.07	0.69±0.04	0.06±0.01	0.12±0.10
Lygus borealis								
Crops *					**Early ***	**Late ***		
Canola	0.64±0.18	0.30±0.19	0.11±0.04	Early	0.38±0.09	0.60±0.09	0.003±0.00	0.01±0.01
				Late	0.36±0.09	0.57±0.11	0.04±0.01	0.03±0.00
Forage	0.21±0.03	0.14±0.06	0.65±0.17	Early	0.29±0.12	0.25±0.02	0.02±0.01	0.45±0.13
				Late	0.14±0.05	0.21±0.03	0.03±0.01	0.62±0.07
Sampling Periods					**Early ***	**Late ***		
172-179	0.51±0.30	0.17±0.17	0.32±0.13	131-171	0.43±0.17	0.52±0.23	0.00±0.00	0.06±0.06
180-186	0.52±0.38	0.10±0.01	0.38±0.37	172-185	0.23±0.06	0.45±0.25	0.01±0.00	0.32±0.31
187-191	0.10±0.10	0.52±0.42	0.39±0.32	186-192	0.35±0.25	0.32±0.07	0.03±0.03	0.32±0.29
192-195	0.57±0.26	0.10±0.07	0.43±0.26	188-196	0.34±0.24	0.25±0.06	0.05±0.01	0.36±0.30
196-205	.	.	.	197-208	0.27±0.02	0.47±0.18	0.04±0.02	0.24±0.22
206-210	.	.	.	209-216	0.14±0.08	0.46±0.30	0.02±0.01	0.39±0.38

* Indicates a significant comparison from Table 9.

mating status frequencies varied between high numbers of females with partly deflated or uninflated seminal depositories (Table 10) (Fig. 22 B). There was a significant interaction between crops and sampling periods (Tables 9 & 11). In general, high numbers of *L. elisus* females in the canola were participating in mating activity across sampling periods compared to females in the forage, as indicated by the varying but relatively high frequencies of females with deflated, partly deflated, or inflated seminal depository (Fig. 22 A & B).

Comparison of *L. borealis* Collected in Canola and Forage Crops. In the comparison of mating status frequencies between the canola and forage crops for *L. borealis* using main effects of crop and sampling periods corresponding to canola growth stages in categorical modelling, sample sizes forming the row or column means in the contingency table varied from 7 to 90 in 1994 (Fig. 22 C), 52 to 282 in early 1995, and 105 to 288 in late 1995 comparisons (Fig. 22 D).

Lygus borealis mating status frequencies were significantly different between individuals collected in the canola and the forage in 1994, early-seeded 1995, and late-seeded 1995 (Table 9) (Fig. 22 C & D). In the canola, high numbers of female *L. borealis* in the canola had partly deflated seminal depositories whereas high numbers of females in the forage were unmated (Table 10) (Fig. 22 C & D). More female *L. borealis* were mated (females with inflated, partly deflated, or deflated seminal depositories) in the canola than in the forage (Table 10) (Fig. 22 C & D). There was no significant difference in mating frequencies between sampling periods in 1994, however there was a significant difference in early and late 1995 (Table 9) (Fig. 22 C & D). In most of the sampling

Table 11: Comparison[1] of female mating status ratios between canola and forage crops and between sampling periods for both *Lygus elisus* and *L. borealis* collected by sweep-net in 1994 and 1995.

	Lygus elisus			*Lygus borealis*		
	χ^2	P	df	χ^2	P	df
1994						
Intercept	196.09	<0.0001	2	243.94	<0.0001	2
Crops[2]						
(Early Rosette)	21.92	<0.0001	2	22.84	<0.0001	2
(Early Bud)	30.16	<0.0001	2	115.30	<0.0001	2
(Early Flower)	135.55	<0.0001	2	84.48	<0.0001	2
(Late Rosette)	1.15	0.56	2	11.40	0.003	2
(Late Bud)	11.09	0.004	2	-	-	-
Sampling Periods [3]	19.78	0.01	8	3.73	0.71	6
Crops x Sampling Periods	.	.	0	.	.	0
1995 Early						
Intercept	785.80	<0.0001	3	1441.04	<0.0001	3
Crops[4]						
(Rosette)	1.57	0.67	3	26.95	<0.0001	3
(Bud)	135.11	<0.0001	3	222.51	<0.0001	3
(Flower)	40.09	<0.0001	3	221.80	<0.0001	3
Sampling Periods	19.84	0.003	6	250.82	<0.0001	6
Crops x Sampling Periods	.	.	0	.	.	0
1995 Late						
Intercept	2090.64	<0.0001	3	3309.54	<0.0001	3
Crops[4]						
(Rosette)	78.24	<0.0001	3	240.70	<0.0001	3
(Bud)	29.15	<0.0001	3	102.45	<0.0001	3
(Flower)	5.45	0.14	3	417.86	<0.0001	3
Sampling Periods	85.33	<0.0001	6	83.48	<0.0001	6
Crops x Sampling Periods	.	.	0	.	.	0

[1] PROC CATMOD (SAS Institute Inc. 1985; 1990) using nested-by-effects (sampling period)

[2] *Brassica napus* cv. Legend and *Medicago sativa* L.

[3] Sampling periods compared in 1994 for *L. elisus* correspond to days 172-179, 180-186, 187-191, 192-195, and 196-205 and for *L. borealis*, correspond to days 172-179, 180-186, 187-191, and 192-195 which avoided comparisons with unbalanced data.

[4] *B. napus* cv. Westar and *Onobrychis viciaefolia* Scop. cv. Nova

periods in 1994, high frequencies of *L. borealis* had seminal depositories which were partly deflated, while less had uninflated, and even lower frequencies had deflated seminal depositories (Table 10) (Fig. 22 C). In 1995, mating status frequencies varied in no consistent pattern between high frequencies of females with partly deflated, uninflated, and inflated seminal depositories (Table 10) (Fig. 22 D). There was a significant interaction between crops and sampling periods (Tables 9 & 11). Similar to *L. elisus*, high numbers of *L. borealis* females in the canola were participating in mating activity across sampling periods compared to females in the forage, as indicated by the varying but relatively high frequencies of females with deflated, partly deflated, or inflated seminal depository (Fig. 22 C & D).

Comparison of *Lygus* species in canola. The sample sizes forming the row or column means in the contingency table varied from 3 to 98 in 1994 (Fig. 22 A & C), 9 to 282 in early 1995, and 102 to 288 in late 1995 (Fig. 22 B & D) when comparing mating status frequencies between the *L. elisus* and *L. borealis* collected in canola using main effects of *Lygus* species and sampling periods corresponding to canola growth stages in categorical modelling.

There was a significant difference in mating frequencies between *L. elisus* and *L. borealis* females collected in the canola in 1994, early 1995 and late 1995 (Table 12) (Fig. 22). Although high frequencies of females of both species had partly deflated seminal depositories, varying frequencies of female *L. elisus* and *L. borealis* had inflated, deflated, or uninflated seminal depositories (Table 13) (Fig. 22). There was a significant difference in female mating status frequencies between sampling periods in the canola in

Table 12: Comparison[1] of female mating status ratios between *Lygus elisus* and *L. borealis* species collected by sweep-net and between sampling periods in both canola and forage crops in 1994 and 1995.

	Canola			Forage		
	χ^2	P	df	χ^2	P	df
1994[2]						
Intercept	40.62	**<0.0001**	2	854.66	**<0.0001**	2
species	12.33	**0.002**	2	0.30	0.86	2
Sampling Periods[3]	19.26	**0.04**	10	9.68	0.14	6
species x Sampling Periods	13.75	0.18	10	16.94	**0.01**	6
1995 Early[4]						
Intercept	793.79	**<0.0001**	3	2792.80	**<0.0001**	3
species	43.75	**<0.0001**	3	70.76	**<0.0001**	3
Sampling Periods	36.84	**<0.0001**	6	387.95	**<0.0001**	6
species x Sampling Periods	8.31	0.22	6	15.75	**0.02**	6
1995 Late[4]						
Intercept	2295.14	**<0.0001**	3	3647.82	**<0.0001**	3
species	38.01	**<0.0001**	3	1.96	0.58	3
Sampling Periods	184.35	**<0.0001**	6	33.77	**<0.0001**	6
species x Sampling Periods	23.62	**<0.0001**	6	28.08	**<0.0001**	6

[1] PROC CATMOD (SAS Institute Inc. 1985; 1990) using main effects (species and sampling period)

[2] *Brassica napus* cv. Legend and *Medicago sativa* L.

[3] Sampling periods compared in 1994 correspond to days 172-179, 180-186, 187-191, 192-195, 196-205, and 206-210 in the canola and 172-179, 180-186, 187-191, and 192-195 in the forage which avoided comparisons with unbalanced data.

[4] *B. napus* cv. Westar and *Onobrychis viciaefolia* Scop. cv. Nova

Table 13: Mean (±SE) female mating status frequencies for *Lygus elisus* and *L. borealis* sweep-net collected in both canola and forage crops during the early-seeded rosette, bud, flower and late-seeded rosette, bud, and flower sampling periods in 1994 and 1995.

	1994				1995			
	Partly Deflated	Deflated	Uninflated		Inflated	Partly Deflated	Deflated	Uninflated
Canola								
***Lygus* species ***					Early *	Late *		
Lygus elisus	0.78±0.06	0.07±0.02	0.15±0.07	Early	0.19±0.05	0.57±0.10	0.10±0.05	0.14±0.06
				Late	0.24±0.07	0.60±0.13	0.06±0.01	0.11±0.05
Lygus borealis	0.75±0.14	0.21±0.13	0.05±0.03	Early	0.38±0.09	0.60±0.10	0.00±0.00	0.01±0.01
				Late	0.36±0.09	0.57±0.11	0.04±0.01	0.03±0.01
Sampling Periods **					Early *	Late *		
172-179	0.81±0.01	0.00±0.00	0.20±0.01	**131-171**	0.38±0.02	0.73±0.02	0.00±0.00	0.00±0.00
180-186	0.81±0.10	0.12±0.03	0.08±0.07	**172-185**	0.19±0.10	0.68±0.02	0.05±0.04	0.09±0.08
187-191	0.44±0.44	0.52±0.42	0.04±0.03	**186-192**	0.39±0.20	0.36±0.03	0.11±0.11	0.14±0.11
192-195	0.67±0.17	0.09±0.09	0.25±0.25	**188-196**	0.49±0.10	0.30±0.01	0.07±0.02	0.14±0.08
196-205	0.91±0.07	0.07±0.05	0.02±0.02	**197-208**	0.20±0.10	0.71±0.07	0.05±0.01	0.06±0.04
206-210	0.94±0.14	0.05±0.00	0.01±0.01	**209-216**	0.22±0.01	0.75±0.02	0.03±0.02	0.02±0.01
Forage								
***Lygus* species**					Early*	Late		
Lygus elisus	0.20±0.04	0.12±0.05	0.68±0.07	Early	0.01±0.02	0.23±0.14	0.03±0.02	0.73±0.13
				Late	0.10±0.01	0.40±0.11	0.04±0.01	0.46±0.12
Lygus borealis	0.21±0.03	0.14±0.06	0.65±0.06	Early	0.29±0.12	0.25±0.02	0.02±0.01	0.45±0.13
				Late	0.14±0.05	0.21±0.03	0.03±0.01	0.62±0.07
Sampling Periods					Early *	Late *		
172-179	0.18±0.03	0.18±0.15	0.64±0.18	**131-171**	0.30±0.30	0.43±0.14	0.00±0.00	0.28±0.16
180-186	0.18±0.04	0.20±0.09	0.62±0.14	**172-185**	0.09±0.09	0.11±0.09	0.02±0.01	0.80±0.18
187-191	0.16±0.05	0.10±0.00	0.75±0.05	**186-192**	0.07±0.03	0.17±0.08	0.07±0.02	0.69±0.09
192-195	0.31±0.00	0.04±0.04	0.66±0.04	**188-196**	0.10±0.00	0.18±0.01	0.03±0.01	0.69±0.03
196-205	.	.	.	**197-208**	0.19±0.07	0.34±0.05	0.03±0.01	0.45±0.00
206-210	.	.	.	**209-216**	0.07±0.01	0.40±0.24	0.05±0.03	0.49±0.27

**Indicates a significant comparison from Table 12.

1994, early 1995, and late 1995 (Table 12) (Fig. 22). In the canola in 1994, high frequencies of females had partly deflated seminal depositories for most of the sampling periods, however, varying frequencies of females had deflated or uninflated seminal depositories and the highest frequencies of unmated females occurred during the rosette sampling periods (Table 13) (Fig. 22 A & C). In 1995, high frequencies of females had either partly deflated or inflated seminal depositories while other mating status frequencies varied between sampling periods examined in the canola (Table 13) (Fig. 22 B & D). There was no significant interaction between *Lygus* species and sampling periods compared in 1994 or early 1995 in the canola (Table 12). In late 1995, there was a significant interaction between species and sampling periods (Table 12). Relatively higher numbers of *L. borealis* than *L. elisus* were participating in mating activity in the canola across sampling periods compared while lower but varying numbers of females had deflated, partly deflated or inflated seminal depositories (Fig. 22 B & D) (Table 14).

Comparison of *Lygus* species in forage. The sample sizes forming the row or column means in the contingency table varied from 13 to 33 in 1994 (Fig. 22A & C), 9 to 151 in early 1995, and 14 to 159 in late 1995 (Fig. 22 B & D) when comparing mating status frequencies between the *L. elisus* and *L. borealis* collected in forage crops using main effects of *Lygus* species and sampling periods corresponding to canola growth stages in categorical modelling.

There was no significant difference between *L. elisus* and *L. borealis* female mating frequencies in the 1994 and early 1995 forage (Table 12) (Fig. 22). In both *Lygus* species, high frequencies of females were unmated and lower, decreasing frequencies of

Table 14: Comparison[1] of female mating status ratios between *Lygus elisus* and *L. borealis* species collected by sweep-net and between sampling periods in both canola and forage crops in 1994 and 1995.

	Canola			Forage		
	χ^2	P	df	χ^2	P	df
1994[2]						
Intercept				766.73	**<0.0001**	2
species						
(Early Rosette)				10.70	**0.05**	2
(Early Bud)				5.19	0.07	2
(Early Flower)				0.99	0.61	2
(Late Rosette)				0.36	0.84	2
Sampling Periods[3]				9.34	0.16	6
species x Sampling Periods				.	.	0
1995 Early[4]						
Intercept				1512.73	**<0.0001**	3
species						
(Rosette)				16.44	**0.0009**	3
(Bud)				53.00	**<0.0001**	3
(Flower)				17.08	**0.0007**	3
Sampling Periods				74.09	**<0.0001**	6
species x Sampling Periods				.	.	0
1995 Late[4]						
Intercept	2241.08	**<0.0001**	3	2771.74	**<0.0001**	3
species						
(Rosette)	17.23	**0.0006**	3	2.11	0.55	3
(Bud)	41.11	**<0.0001**	3	5.13	0.16	3
(Flower)	3.27	0.35	3	22.79	**<0.0001**	3
Sampling Periods	187.77	**<0.0001**	6	31.60	**<0.0001**	6
species x Sampling Periods	.	.	0	.	.	0

[1] PROC CATMOD (SAS Institute Inc. 1985; 1990) using nested-by-effects (sampling period)
[2] *Brassica napus* cv. Legend and *Medicago sativa* L.
[3] Sampling periods compared in 1994 correspond to days 172-179, 180-186, 187-191, 192-195, 196-205, and 206-210 in the canola and 172-179, 180-186, 187-191, and 192-195 in the forage which avoided comparisons with unbalanced data.
[4] *B. napus* cv. Westar and *Onobrychis viciaefolia* Scop. cv. Nova

females had partly deflated then deflated seminal depositories in 1994 (Table 13) (Fig. 22 A & C). In early 1995 in the forage, *L. elisus* and *L. borealis* frequencies of uninflated females were most frequent and lower, decreasing frequencies of partly deflated, inflated, and deflated females, respectively, were generally observed (Table 13) (Fig. 22 B & D). In late 1995, even though high frequencies of female *L. elisus* and *L. borealis* were unmated, higher frequencies of *L. borealis* were unmated than *L. elisus* and lower frequencies of *L. borealis* had partly deflated seminal depositories compared to *L. elisus* collected in the forage (Table 13) (Fig. 22 B & D). There was no significant difference in mating status frequencies between sampling periods compared in 1994 but there was a significant difference in both the early 1995 and late 1995 sampling periods in the forage (Table 12). In 1994, high numbers of females in the forage had uninflated seminal depositories and low numbers of females had partly deflated and deflated seminal depositories (Table 13) (Fig. 22 A). In early 1995, high frequencies of females had partly deflated seminal depositories in the forage at the rosette sampling period and by the bud and flower sampling periods, high frequencies of females had uninflated seminal depositories (Table 13) (Fig. 22 B & D). In addition, varying frequencies of females with inflated seminal depositories were observed (Table 13) (Fig. 22 B & D). In the forage in late 1995, high frequencies of females consistently had uninflated seminal depositories in the rosette, bud, and flower sampling periods, however, frequencies of females with inflated, and partly deflated seminal depositories fluctuated between sampling periods (Table 13) (Fig. 22 B & D). There was a significant interaction between *Lygus* species and sampling periods in 1994, early 1995, and late 1995 (Tables 12 & 14). With one

exception in the early sampling period, generally low numbers of *Lygus* females were participating in mating activity, as indicated by an uninflated seminal depository (Fig. 22). In 1994, significantly higher numbers of *L. elisus* were categorized as reproductively immature because they had uninflated seminal depositories compared to *L. borealis*. However varying frequencies of females in both species had deflated, or partly deflated seminal depositories across the sampling periods compared (Fig. 22 A & C). Similarly, in early sampling periods compared in 1995, high frequencies of female *L. elisus* were immature, indicated by the presence of an uninflated seminal depository, compared to *L. borealis* but similarly varying frequencies of females of both species had deflated, partly deflated, or inflated seminal depositories. In the late sampling periods compared in 1995, a greater number of *L. borealis* females than *L. elisus* were immature in the forage (Fig. 22 B & D, Late). However, varying numbers of females in both species had deflated, partly deflated, or inflated seminal depositories across the periods compared.

4.4.3 Female Egg Development Status

Females characterized as non-reproductive were observed in field collections in 1994 but none were collected in 1995.

Comparison of *L. elisus* Collected in Canola and Forage Crops. When comparing egg development frequencies between the canola and forage crops for *L. elisus* using main effects of crop and sampling periods corresponding to canola growth stages in categorical modelling, sample sizes forming the row or column means in the contingency table varied from 5 to 100 in 1994 (Fig. 23 A), 8 to 69 in early 1995, and 14 to 229 in late

1995 comparisons (Fig. 23 B).

There was a consistent, significant difference in *L. elisus* egg development frequencies between canola and forage crops in 1994, early 1995, and late 1995 (Table 15) (Fig. 23 A & B). In the canola, high frequencies of *L. elisus* contained chorionated oocytes and higher frequencies of *L. elisus* had chorionated oocytes in the canola than in the forage (Table 16) (Fig. 23 A & B). In the 1994 forage, females characterized as vitellogenic, previtellogenic, post-ovipositional, and non-reproductive were present (Table 16) (Fig. 23 A). In 1995, higher frequencies of *L. elisus* had chorionated oocytes in their ovarioles in the canola whereas in the forage, high frequencies of females were characterized as previtellogenic in early 1995, while equal frequencies of chorionated and previtellogenic females were present in the late 1995 forage (Table 16) (Fig. 23 B). There was a significant difference in *L. elisus* egg development frequencies between sampling periods (Table 15). Within each sampling period in 1994, the highest frequencies were generally for females with chorionated oocytes (Table 16) (Fig. 23 A). Lower frequencies of non-reproductive, previtellogenic, vitellogenic, or post-ovipositional females were observed in different sampling periods but varied in no specific pattern between sampling periods (Table 16) (Fig. 23 A). In early 1995, differences between the frequencies of chorionated and previtellogenic female *L. elisus* contributed to significant differences between sampling periods. High numbers of females contained chorionated oocytes at the rosette sampling period but high frequencies of previtellogenic females were present in the bud and flower sampling periods (Table 16) (Fig. 23 B). Within individual sampling periods in late 1995, the highest frequencies

Table 15: Comparison[1] of female egg development stages between canola and forage crops and between sampling periods for both *Lygus elisus* and *L. borealis* collected by sweep-net in 1994 and 1995.

	Lygus elisus			*Lygus borealis*		
	χ^2	P	df	χ^2	P	df
1994						
Intercept	1221.97	**<0.0001**	4	1094.83	**<0.0001**	4
Crops[2]	597.30	**<0.0001**	4	606.53	**<0.0001**	4
Sampling Periods[3]	42.32	**0.0004**	16	6.18	0.91	12
Crops x Sampling Periods	61.63	**<0.0001**	16	8.26	0.76	12
1995 Early						
Intercept	1489.07	**<0.0001**	3	44851.30	**<0.0001**	3
Crops[4]	104.07	**<0.0001**	3	266.58	**<0.0001**	3
Sampling Periods	22.35	**<0.0001**	6	14.51	**<0.0001**	6
Crops x Sampling Periods	12.80	**0.05**	6	71.43	**<0.0001**	6
1995 Late						
Intercept	28272.94	**<0.0001**	3	128217.14	**<0.0001**	3
Crops[4]	57.57	**<0.0001**	3	661.55	**<0.0001**	3
Sampling Periods	49.66	**<0.0001**	6	9.79	0.14	6
Crops x Sampling Periods	4.59	0.60	6	29.04	**<0.0001**	6

[1] PROC CATMOD (SAS Institute Inc. 1985; 1990) using main effects (crops and sampling period)

[2] *Brassica napus* cv. Legend and *Medicago sativa* L.

[3] Sampling periods compared in 1994 for *L. elisus* correspond to days 172-179, 180-186, 187-191, 192-195, and 196-205 and for *L. borealis*, correspond to days 172-179, 180-186, 187-191, and 192-195 which avoided comparisons with unbalanced data.

[4] *B. napus* cv. Westar and *Onobrychis viciaefolia* Scop. cv. Nova

Table 16: Mean (±SE) female egg development frequencies for *Lygus elisus* characterized as vitellogenic (Vit), chorionated (Chor), post-ovipositional (Post), previtellogenic (Pre), or non-reproductive (Non-repro) collected by sweep-net in canola and forage crops during the early-seeded rosette, bud, flower, and late-seeded rosette, bud, flower sampling periods in 1994 and 1995.

	1994						1995			
	Vit	Chor	Post	Pre	Non-repro		Vit	Chor	Post	Pre
Crops *							**Early ***	**Late ***		
Canola	0.09±0.03	0.76±0.07	0.14±0.08	0.01±0.01	0.00±0.00	**Early**	0.06±0.03	0.76±0.11	0.00±0.00	0.18±0.08
						Late	0.05±0.02	0.82±0.07	0.00±0.00	0.13±0.06
Forage	0.35±0.06	0.03±0.01	0.44±0.10	0.05±0.02	0.18±0.10	**Early**	0.02±0.02	0.25±0.12	0.00±0.00	0.73±0.26
						Late	0.01±0.01	0.49±0.06	0.00±0.00	0.49±0.06
Sampling Periods *							**Early ***	**Late ***		
172-179	0.20±0.00	0.42±0.39	0.05±0.05	0.02±0.02	0.32±0.32	**131-171**	0.00±0.00	0.75±0.25	0.00±0.00	0.25±0.25
180-186	0.29±0.15	0.37±0.34	0.24±0.13	0.08±0.05	0.02±0.01	**172-185**	0.03±0.03	0.37±0.35	0.00±0.00	0.60±0.38
187-191	0.16±0.06	0.44±0.41	0.40±0.35	0.02±0.02	0.02±0.02	**186-192**	0.09±0.03	0.40±0.16	0.00±0.00	0.52±0.19
192-195	0.15±0.15	0.25±0.25	0.52±0.02	0.00±0.00	0.08±0.08	**188-196**	0.05±0.03	0.50±0.15	0.01±0.01	0.44±0.19
196-205	0.30±0.28	0.49±0.44	0.23±0.19	0.03±0.03	0.03±0.03	**197-208**	0.02±0.00	0.71±0.15	0.00±0.00	0.27±0.16
206-210	.	.	.	.	.	**209-216**	0.01±0.01	0.77±0.18	0.00±0.00	0.22±0.20

* Indicates a signficant comparison from Table 15.

observed were for females with chorionated oocytes with lower frequencies of females containing previtellogenic oocytes (Table 16) (Fig. 23 B). With little variation occurring between sampling periods for vitellogenic and post-ovipositional females, the significant differences likely were caused by changes in frequencies of chorionated and previtellogenic females between sampling periods compared in 1995 (Table 16) (Fig. 23 B). There was a significant interaction between canola and forage crops and sampling periods in 1994 and early 1995 but no significant interaction occurred in late 1995 (Table 15). In 1994, the significant interaction was related to high but varying frequencies of chorionated females in the canola compared to varying frequencies of vitellogenic, post-ovipositional or non-reproductive females in the forage across sampling periods compared (Fig. 23 A) (Table 17). In early 1995, the significant interaction was related to a greater number of chorionated females in the canola than in the forage where varying frequencies of predominantly previtellogenic females but also vitellogenic and chorionated females were present across sampling periods compared (Fig. 23B) (Table 17).

Comparison of *L. borealis* Collected in Canola and Forage Crops. In the comparison of egg development frequencies between the canola and forage crops for *L. borealis* using main effects of crop and sampling periods corresponding to canola growth stages in categorical modelling, sample sizes forming the row or column means in the contingency table varied from 9 to 91 in 1994 (Fig. 23 C), 53 to 282 in early 1995, and 105 to 283 in late 1995 comparisons (Fig. 23 D).

There was a significant difference in *L. borealis* egg development frequencies

Table 17: Comparison[1] of female egg development stages between canola and forage crops and between sampling periods for both *Lygus elisus* and *L. borealis* collected by sweep-net in 1994 and 1995.

	Lygus elisus			*Lygus borealis*		
	χ^2	P	df	χ^2	P	df
1994						
Intercept	732.45	**<0.0001**	4			
Crops[2]						
(Early Rosette)	33.69	**<0.0001**	4			
(Early Bud)	143.21	**<0.0001**	1			
(Early Flower)	196.45	**<0.0001**	4			
(Late Rosette)	2.18	0.70	4			
(LateBud)	283.39	**<0.0001**	4			
Sampling Periods[3]	67.16	**<0.0001**	16			
Crops x Sampling Periods	.	.	0			
1995 Early						
Intercept	1326.21	**<0.0001**	3	41671.03	**<0.0001**	3
Crops[4]						
(Rosette)	2.61	0.46	3	4.57	0.21	3
(Bud)	98.85	**<0.0001**	3	195.25	**<0.0001**	3
(Flower)	15.41	**0.002**	3	138.20	**<0.0001**	3
Sampling Periods	12.49	**0.05**	6	68.14	**<0.0001**	6
Crops x Sampling Periods	.	.	0	.	.	0
1995 Late						
Intercept				113836.44	**<0.0001**	3
Crops[4]						
(Rosette)				165.55	**<0.0001**	3
(Bud)				107.10	**<0.0001**	3
(Flower)				417.95	**<0.0001**	3
Sampling Periods				29.05	**0.0001**	6
Crops x Sampling Periods				.	.	0

[1] PROC CATMOD (SAS Institute Inc. 1985; 1990) using nested-by-effects (sampling period)

[2] *Brassica napus* cv. Legend and *Medicago sativa* L.

[3] Sampling periods compared in 1994 for *L. elisus* correspond to days 172-179, 180-186, 187-191, 192-195, and 196-205 and for *L. borealis*, correspond to days 172-179, 180-186, 187-191, and 192-195 which avoided comparisons with unbalanced data.

[4] *B. napus* cv. Westar and *Onobrychis viciaefolia* Scop. cv. Nova

between canola and forage crops in 1994, early 1995, and late 1995 (Table 15) (Fig. 23 B & D). High frequencies of female *L. borealis* had chorionated oocytes in both years and higher frequencies of females with chorionated oocytes were observed in the canola compared to the forage (Table 18) (Fig. 23 B & D). In 1994, high frequencies of post-ovipositional female *L. borealis* were present in the forage, followed by vitellogenic females whereas in the canola, the majority of female *L. borealis* contained chorionated oocytes (Table 18) (Fig. 23 B). In early 1995, the highest frequencies of *L. borealis* females had chorionated oocytes in both canola and forage however, in the forage, approximately half the frequency of females with chorionated oocytes were present and relatively high frequencies of females were characterized as previtellogenic (Table 18) (Fig. 23 D). In late 1995, the highest frequencies of female *L. borealis* in both crops were chorionated in the canola and previtellogenic in the forage, although, frequencies of females with chorionated oocytes were relatively high in forage (Table 18) (Fig. 23 D). There was no significant difference in egg development frequencies between sampling periods in 1994 and late 1995, however, there was a significant difference between sampling periods in early 1995 (Table 17). The absence of significant differences between sampling periods is related to stable patterns between sampling periods in egg development where high frequencies of females were characterized in 1994 as chorionated, followed by lower, decreasing frequencies of post-ovipositional, vitellogenic, previtellogenic, and non-reproductive, respectively (Table 18) (Fig. 23 B). In late 1995, the pattern consisted mainly of high frequencies of female *L. borealis* characterized as chorionated, followed by lower frequencies of females which were

Table 18: Mean (±SE) female egg development frequencies for *Lygus borealis* characterized as vitellogenic (Vit), chorionated (Chor), post-ovipositional (Post), previtellogenic (Pre), or non-reproductive (Non-repro) collected by sweep-net in canola and forage crops during the early rosette, bud, flower, and late rosette, bud, flower sampling periods in 1994 and 1995.

	1994						1995			
	Vit	Chor	Post	Pre	Non-repro		Vit	Chor	Post	Pre
Crops *							**Early ***	**Late ***		
Canola	0.05±0.02	0.85±0.02	0.09±0.03	0.01±0.01	0.00±0.00	**Early**	0.00±0.00	0.99±0.01	0.00±0.00	0.01±0.01
						Late	0.02±0.02	0.96±0.02	0.00±0.00	0.03±0.02
Forage	0.27±0.01	0.01±0.01	0.62±0.04	0.07±0.04	0.03±0.02	**Early**	0.03±0.03	0.56±0.13	0.00±0.00	0.42±0.12
						Late	0.02±0.01	0.35±0.07	0.00±0.00	0.62±0.07
Sampling Periods							**Early ***	**Late**		
172-179	0.14±0.10	0.43±0.39	0.33±0.23	0.08±0.04	0.02±0.02	**131-171**	0.00±0.00	0.94±0.06	0.00±0.00	0.06±0.06
180-186	0.18±0.07	0.42±0.42	0.39±0.35	0.01±0.01	0.00±0.00	**172-185**	0.02±0.02	0.69±0.31	0.00±0.00	0.30±0.30
187-191	0.16±0.11	0.45±0.45	0.31±0.26	0.08±0.08	0.00±0.00	**186-192**	0.03±0.03	0.69±0.28	0.00±0.00	0.29±0.26
192-195	0.16±0.16	0.42±0.42	0.31±0.21	0.00±0.00	0.05±0.05	**188-196**	0.02±0.01	0.63±0.29	0.00±0.00	0.35±0.28
196-205	.	.	.	.	.	**197-208**	0.01±0.01	0.75±0.24	0.00±0.00	0.24±0.23
206-210	.	.	.	.	.	**209-216**	0.01±0.01	0.60±0.39	0.01±0.00	0.39±0.38

* Indicates a significant comparison from Table 15.

previtellogenic (Table 18) (Fig. 23 D). There was no significant interaction between canola and forage crops and sampling periods in 1994 (Table 15). However, in both early and late 1995, there was a significant interaction between crops and sampling periods compared (Table 15). In early 1995, high numbers of females in the canola had chorionated oocytes but varying numbers of females in the forage had chorionated, vitellogenic and previtellogenic oocytes across the sampling periods compared (Fig. 23D, Early). Similarly, high numbers of females in the canola had chorionated oocytes but the frequencies of females with previtellogenic and chorionated oocytes present in the forage varied across sampling periods compared (Fig. 23 D, Late) (Table 17).

Comparison of *Lygus* species Collected in Canola. The sample sizes forming the row or column means in the contingency table varied from 5 to 100 in 1994 (Fig. 23 A & C), 10 to 282 in early1995, and 103-283 in late 1995 (Fig. 23 B & D) when comparing egg development frequencies between the *L. elisus* and *L. borealis* collected in canola using main effects of *Lygus* species and sampling periods corresponding to canola growth stages in categorical modelling.

There was no significant difference in egg development frequencies between *L. elisus* and *L. borealis* females collected in the 1994 canola but there was a significant difference in early and late 1995 (Table 19) (Fig. 23). In 1994, high frequencies of females in both *Lygus* species contained chorionated oocytes with lower, decreasing frequencies following a similar pattern from post-ovipositional, vitellogenic, previtellogenic to non-reproductive, respectively (Table 20) (Fig. 23 A & C). In early and late 1995, a pattern of high frequencies of chorionated, followed by lower, decreasing

Table 19: Comparison[1] of female egg development stages between *Lygus elisus* and *L. borealis* species collected by sweep-net and between sampling periods in both canola and forage crops in 1994 and 1995.

	Canola			Forage		
	χ^2	P	df	χ^2	P	df
1994[2]						
Intercept	2725.79	<0.0001	4	279.92	<0.0001	4
species	2.65	0.62	4	10.20	**0.04**	4
Sampling Periods[3]	37.37	**0.01**	20	25.54	**0.01**	12
species x Sampling Periods	9.99	0.97	20	47.91	<0.0001	12
1995 Early[4]						
Intercept	7445.78	<0.0001	3	17499.67	<0.0001	3
species	35.07	<0.0001	3	71.78	<0.0001	3
Sampling Periods	5.02	0.54	6	103.64	<0.0001	6
species x Sampling Periods	3.79	0.71	6	8.64	0.20	6
1995 Late[4]						
Intercept	108546.73	<0.0001	3	29661.57	<0.0001	3
species	29.39	<0.0001	3	2.36	0.50	3
Sampling Periods	30.46	<0.0001	6	29.33	<0.0001	6
species x Sampling Periods	25.31	<0.0001	6	7.99	0.24	6

[1] PROC CATMOD (SAS Institute Inc. 1985; 1990) using main effects (species and sampling period)

[2] *Brassica napus* cv. Legend and *Medicago sativa* L.

[3] Sampling periods compared in 1994 correspond to days 172-179, 180-186, 187-191, 192-195, 196-205, and 206-210 in the canola and 172-179, 180-186, 187-191, and 192-195 in the forage which avoided comparisons with unbalanced data.

[4] *B. napus* cv. Westar and *Onobrychis viciaefolia* Scop. cv. Nova

Table 20: Mean (±SE) female egg development frequencies for *Lygus elisus* and *L. borealis* characterized as vitellogenic (Vit), chorionated (Chor), post-ovipositional (Post), previtellogenic (Pre), or non-reproductive (Non-repro) collected by sweep-net in canola during the early rosette, bud, flower, and late rosette, bud, flower sampling periods in 1994 and 1995.

	1994						1995			
	Vit	Chor	Post	Pre	Non-repro		Vit	Chor	Post	Pre
***Lygus* species**							**Early ***	**Late ***		
L. elisus	0.08±0.03	0.79±0.06	0.13±0.07	0.01±0.01	0.00±0.00	**Early**	0.06±0.03	0.76±0.11	0.00±0.00	0.18±0.08
						Late	0.05±0.02	0.82±0.07	0.01±0.01	0.13±0.06
L. borealis	0.05±0.01	0.87±0.02	0.07±0.02	0.01±0.01	0.00±0.00	**Early**	0.00±0.00	0.99±0.01	0.00±0.00	0.01±0.01
						Late	0.003±0.00	0.96±0.02	0.01±0.01	0.03±0.02
Sampling Periods *							**Early**	**Late ***		
172-179	0.12±0.08	0.81±0.01	0.05±0.05	0.02±0.02	0.00±0.00	**131-171**	0.00±0.00	1.00±0.00	0.00±0.00	0.00±0.00
180-186	0.12±0.01	0.78±0.07	0.07±0.04	0.02±0.01	0.01±0.01	**172-185**	0.03±0.03	0.85±0.14	0.00±0.00	0.11±0.10
187-191	0.08±0.03	0.88±0.03	0.05±0.00	0.00±0.00	0.00±0.00	**186-192**	0.06±0.06	0.76±0.21	0.00±0.00	0.18±0.15
192-195	0.00±0.00	0.67±0.17	0.33±0.17	0.00±0.00	0.00±0.00	**188-196**	0.05±0.04	0.79±0.13	0.01±0.01	0.16±0.09
196-205	0.04±0.02	0.93±0.01	0.04±0.01	0.00±0.00	0.00±0.00	**197-208**	0.01±0.01	0.92±0.06	0.00±0.00	0.06±0.05
206-210	0.02±0.02	0.92±0.01	0.06±0.01	0.00±0.00	0.00±0.00	**209-216**	0.01±0.01	0.97±0.01	0.01±0.01	0.01±0.01

* Indicates a significant comparison from Table 19.

frequencies of previtellogenic, vitellogenic, and post-ovipositional females was present, although, higher frequencies of *L. borealis* contained chorionated oocytes and lower frequencies contained previtellogenic oocytes compared to *L. elisus* (Table 20) (Fig. 23 B & D). There was a significant difference in egg development frequencies between sampling periods in 1994, and late 1995 but there was no significant difference in early 1995 (Table 19). In 1994, high numbers of females had chorionated oocytes but the number of females with vitellogenic or characterized as post-ovipositional varied between sampling periods (Table 20) (Fig. 23 A & C). In late 1995, high frequencies of females had chorionated oocytes, although the frequencies varied and the frequencies of previtellogenic females varied between sampling periods (Table 20) (Fig. 23 B & D). In early 1995, the high frequencies of females with chorionated oocytes and lower, decreasing frequencies of previtellogenic, and vitellogenic oocytes did not change between sampling periods compared (Table 20) (Fig. 23 B & D). There was no significant interaction between *L. elisus* and *L. borealis* egg development frequencies and sampling periods in 1994, and early 1995, however, there was a significant interaction in late 1995 (Table 19). High and increasing frequencies of *L. elisus* had chorionated oocytes although more *L. borealis* had chorionated across sampling periods compared (Fig. 23 B & D, Late) (Table 21). More *L. elisus* had vitellogenic or previtellogenic oocytes which fluctuated over the sampling periods compared to *L. borealis* which had very few, although varying numbers of vitellogenic or previtellogenic oocytes (Fig. 23 B & D, Late) (Table 21).

Comparison of *Lygus* species Collected in Forage Crops. The sample sizes

Table 21: Comparison[1] of female egg development stages between *Lygus elisus* and *L. borealis* species collected by sweep-net and between sampling periods in both canola and forage crops in 1994 and 1995.

	Canola			Forage		
	χ^2	P	df	χ^2	P	df
1994[2]						
Intercept				252.53	<0.0001	4
species						
(Early Rosette)				46.20	<0.0001	4
(Early Bud)				7.38	0.12	4
(Early Flower)				3.61	0.46	4
(Late Rosette)				0.92	0.92	4
Sampling Periods				44.09	<0.0001	12
species x Sampling Periods				.	.	0
1995 Late[3]						
Intercept	104690.99	<0.0001	3			
species						
(Rosette)	26.91	<0.0001	3			
(Bud)	26.35	<0.0001	3			
(Flower)	1.44	0.70	3			
Sampling Periods	51.26	<0.0001	6			
species x Sampling Periods	.	.	0			

[1] PROC CATMOD (SAS Institute Inc. 1985; 1990) using nested-by-effects (sampling period)

[2] *Brassica napus* cv. Legend and *Medicago sativa* L.

[3] Sampling periods compared in 1994 correspond to days 172-179, 180-186, 187-191, 192-195, 196-205, and 206-210 in the canola and 172-179, 180-186, 187-191, and 192-195 in the forage which avoided comparisons with unbalanced data.

[4] *B. napus* cv. Westar and *Onobrychis viciaefolia* Scop. cv. Nova

forming the row or column means in the contingency table varied from 15 to 34 in 1994 (Fig. 23 A & C), 8 to 136 in early 1995, and 14 to 145 in late 1995 (Fig. 23 B & D) when comparing egg development frequencies between the *L. elisus* and *L. borealis* collected in forage crops using main effects of *Lygus* species and sampling periods corresponding to canola growth stages in categorical modelling.

There was no significant difference between *L. elisus* and *L. borealis* egg development frequencies in the 1994 forage and late 1995 forage, but, there was a significant difference in the early 1995 forage (Table 19) (Fig. 23). A similar pattern consisting of high frequencies of post-ovipositional females, then lower, decreasing frequencies of vitellogenic, non-reproductive, previtellogenic, and chorionated females, respectively, were observed in both *L. elisus* and *L. borealis* in the forage in 1994 (Table 22) (Fig. 23 A & C). In late 1995, similar frequencies of females characterized with relatively equal previtellogenic and chorionated oocytes, and lower frequencies of vitellogenic and post-ovipositional females were present in the forage (Table 22) (Fig. 23 B & D). In early 1995, the pattern of egg development frequencies was not consistent in the forage with relatively equal frequencies of *L. borealis* which were characterized as chorionated and previtellogenic compared to high frequencies of *L. elisus* characterized as previtellogenic followed by lower frequencies of chorionated females. *L. borealis* and high frequencies of previtellogenic, then lower frequencies of chorionated *L. elisus* (Table 22) (Fig. 23 B & D). There was a significant interaction between *Lygus* species compared and sampling periods (Table 19) related to a significant difference in egg development frequencies between *Lygus* species in the early rosette, early bud, early

Table 22: Mean (±SE) female egg development frequencies for *Lygus elisus* and *L. borealis* characterized as vitellogenic (Vit), chorionated (Chor), post-ovipositional (Post), previtellogenic (Pre), or non-reproductive (Non-repro) collected by sweep-net in forage during the early rosette, bud, flower, and late rosette, bud, flower sampling periods in 1994 and 1995.

	1994						1995			
	Vit	Chor	Post	Pre	Non-repro		Vit	Chor	Post	Pre
***Lygus* species**							**Early ***	**Late**		
L. elisus	0.29±0.05	0.02±0.01	0.44±0.12	0.05±0.02	0.20±0.13	**Early**	0.02±0.02	0.25±0.11	0.00±0.00	0.73±0.11
						Late	0.01±0.01	0.50±0.06	0.00±0.00	0.49±0.06
L. borealis	0.27±0.01	0.01±0.01	0.62±0.04	0.07±0.04	0.03±0.02	**Early**	0.03±0.01	0.56±0.13	0.00±0.00	0.42±0.12
						Late	0.02±0.00	0.35±0.07	0.00±0.00	0.62±0.07
Sampling Periods							**Early ***	**Late ***		
172-179	0.22±0.02	0.04±0.01	0.33±0.23	0.08±0.05	0.34±0.30	**131-171**	0.00±0.00	0.69±0.19	0.00±0.00	0.31±0.19
180-186	0.34±0.10	0.02±0.02	0.56±0.19	0.06±0.07	0.02±0.02	**172-185**	0.02±0.02	0.20±0.18	0.00±0.00	0.79±0.20
187-191	0.24±0.03	0.00±0.00	0.66±0.09	0.10±0.07	0.00±0.00	**186-192**	0.05±0.01	0.32±0.09	0.00±0.00	0.62±0.08
192-195	0.31±0.00	0.00±0.00	0.57±0.03	0.00±0.00	0.12±0.03	**188-196**	0.03±0.00	0.34±0.00	0.00±0.00	0.63±0.00
196-205	.	.	.	.	.	**197-208**	0.02±0.00	0.53±0.02	0.00±0.00	0.44±0.02
206-210	.	.	.	.	.	**209-216**	0.01±0.01	0.40±0.19	0.00±0.00	0.59±0.18

* Indicates a significant comparison from Table 19.

flower, and late rosette sampling periods in 1994 (Table 21). All five egg development stages were present in both *L. elisus* and *L. borealis*. However, frequencies of non-reproductive, post-ovipositional, previtellogenic, or vitellogenic females in both species fluctuated across sampling periods with a general trend of low, decreasing frequencies of chorionated females early in the year (Fig. 23, A & C). No significant interaction between *Lygus* species and sampling periods was observed in either the early or late 1995 forage (Table 19).

4.5 Discussion

This study compared *L. elisus* and *L. borealis* sex ratios, and mating status and egg development of females collected in annually sown canola with those of insects collected in perennial forage crops in southern Alberta. These two types of crops were examined because *Lygus* utilize each as a host at some point in the season even though the crop phenologies are quite different. Perennial forage crops commence production of vegetative growth as early as April while commercial crops of annual canola are seeded in late April to late-May in southern Alberta. Forage crops, which may provide overwintering refugia for *Lygus* adults, are available to *Lygus* for at least one month before canola is at the rosette stage of development. Salt (1945) recorded one peak of *Lygus* adults present in alfalfa crops from 20 May to 07 June, a second peak of adults are present in alfalfa from 25 June to 25 July. In 1994, my study period was from 27 June to 14 July and in 1995 from 11 May to 23 August. Therefore, based on Salt's (1945) sweep-net collections in alfalfa, my study examined adults from the second generation in

forage and adults in the canola for comparable time periods in southern Alberta.

4.5.1 Sex Ratios

Overall, no pattern was evident in sex ratio comparisons between *Lygus* in canola and forage crops or between *L. elisus* and *L. borealis*. Statistical differences were present in the periods studied but the only relatively consistent results which were biologically relevant in all the comparisons is that sex ratios changed in different patterns over the sampling periods compared. Male biassed sex ratios have been found in *L. lineolaris* collected by tanglefoot traps in birdsfoot trefoil (*Lotus corniculus* L.) (Ridgeway and Gyrisco 1960). However, in this species, the sex ratio produced in colony reared eggs is 1:1 (Fleischer and Gaylor 1988). The results from this study may be an artifact of the periods utilized in comparisons. Another possibility is that *Lygus* species participated in movement which results in sex ratio fluctuations between sampling periods in these two host crops. Furthermore, because sex ratios were significantly deviating towards both male and female biassed populations in the host crops studied, both sexes likely participated in dispersal but with varying intensity for the two sexes. The dispersal likely occurred continuously during the periods compared and was apparent in the time periods studied as continuing, variable fluctuations in sex ratios in both species.

4.5.2 Female Mating Status

Lygus did not synchronize their mating to a specific canola crop stage. The female mating results for both *L. elisus* and *L. borealis* showed no synchronization with

the rosette, bud, or flower crop stages that were examined in the early or late sampling periods in the canola. Instead, fluctuations in female mating status frequencies that occurred did so over the entirety of the period studied.

Female *L. elisus* and *L. borealis* mating status were different in forage and canola over identical sampling periods. Most *L. elisus* and *L. borealis* females were mated in canola whereas relatively few were mated in forage. Low ratios of mated females in forage suggests that mated females moved out of forage. On the other hand, the high frequencies of mated females collected even in the early crop stages of canola suggests that females moving into the canola crop were already mated. *Lygus hesperus* females are not receptive to mating until 6-8 days following adults eclosion (Strong et al. 1970). That high numbers of females of both *L. elisus* and *L. borealis* were unmated in forage but mated in canola during identical sampling periods suggests that females in forage crops were younger than females in the canola. This therefore, suggests that females were maturing in the forage crop and then moving to canola after mating. Stewart and Gaylor (1994b) found evidence supporting movement of reproductive, parous *L. lineolaris* females from flight mill experiments where early-reproductive (4.5-8.5 d old, maintained at 22-27°C) females exhibit longer cumulative-flight periods than pre-reproductive (3.5-7.5 d old) females. Late reproductive (>14.5 d old) females have cumulative-flights which are seven times longer than flights by less mature females (Stewart and Gaylor 1994b). In an earlier study Stewart and Gaylor (1991) found that <6.6% of female *L. lineolaris* moving to patches of mustard (*Brassica juncea crispifolia* L.) are unmated. More direct studies of movement in *L. elisus* and *L. borealis* are needed

to prove that there is actually dispersal of mature females from forages to canola.

4.5.3 Egg Development

Egg development in *Lygus* occurred independent of canola crop stage, although significant differences in egg development frequencies occurred between early and late seeded stands of canola. Egg development in *L. elisus* followed no seasonal pattern from June to early August. Initially, most females contained chorionated oocytes. Later, fewer females contained chorionated oocytes (21 June - 11 July) but increasing numbers contained chorionated oocytes in late sampling in early August. This study found no seasonal pattern in *L. borealis* egg development. There also was no difference in egg development frequencies between early and late seeded stands of canola. High numbers of female *L. borealis* contained chorionated oocytes for the duration of the study period. In southern Manitoba, a ratio of ≥0.80 of *L. lineolaris* females contain chorionated oocytes in canola (*B. napus*) during the sampling periods used in this study (Gerber and Wise 1995). Therefore, *L. elisus*, *L. borealis*, and *L. lineolaris* show no seasonal egg development pattern. Moreover, all three species developed eggs independent of canola crop stages.

The incidence of *Lygus* females at various stages of egg development in canola and forage crops strongly suggests that egg development and oviposition were related to which females participated in dispersal events and possibly even which host is selected. In southern Manitoba, the stage of egg development in field collected females of *L. lineolaris* from alfalfa (*M. sativa* L.), and ever-bearing strawberries (*Fragaria* x *ananassa*

Duchesne) is slightly different than that of females collected from canola (*B. napus* L.). In alfalfa and ever-bearing strawberries, high ratios of females contain previtellogenic oocytes in mid-June and are gradually replaced by high ratios of females containing chorionated oocytes in early August (Gerber and Wise 1995). During comparable sampling periods in canola, high ratios of females (>0.80) contain chorionated oocytes from early July until early August (Gerber and Wise 1995). From early August onwards, second generation female *L. lineolaris* with previtellogenic oocytes begin to replace females with chorionated oocytes (Gerber and Wise 1995). Thus, in southern Manitoba, *L. lineolaris* egg development appears to be similar in forage, ever-bearing strawberries, and canola until early August when higher ratios of females contain chorionated oocytes in the canola compared to alfalfa and strawberries. The same is the case in southern Alberta where *L. elisus* and *L. borealis* females, based on stage of egg development, were ready to oviposit in canola but not ready to oviposit in forage crops. Spring seeded canola has not been shown to be an overwintering habitat for *Lygus* in Canada and it is presumably unavailable until the cotyledons develop. Oviposition likely commences at the rosette stage and continues until the plant is no longer suitable to the female or the plant cut for harvest. Therefore, adult *Lygus* present in canola stands prior to early flowering must arise from adult movement to the canola.

Studies have shown that *Lygus* feeding and oviposition host preferences may not be identical for different species. Gerber (1995) found that *L. lineolaris* discern between genus and species of host plants. *Lygus lineolaris* prefer to oviposit on *Sinapis*, then later in *Brassica*, in choice tests. In addition, *L. lineolaris* prefer *B. carinata* and *B. napus* to

B. juncea, and *S. alba* to *S. arvensis*. *Lygus lineolaris* also exhibit an oviposition preference for fleabane (*Erigeron strigosus* Muhlenberg ex. Willdenow) over cotton (*Gossypium hirsutum* L.) (Stewart and Gaylor 1994b). Even though green beans are a superior diet for nymphal development, *L. lineolaris* prefer to oviposit on celery or carrots over green beans (Curtis and McCoy 1964). These studies indicate that *L. lineolaris* select between hosts and that host selection is different for oviposition and feeding. Likely *L. elisus* and *L. borealis* exhibit the same ability to distinguish between hosts. Results from this study show that high frequencies of *L. elisus* and *L. borealis* females in canola were ready to oviposit whereas high frequencies of females in forage crops were not ready to oviposit. If dispersal is an adaptation to locate oviposition sites as opposed to strictly locating a food source, and *Lygus* are able to distinguish between hosts, females ready to oviposit may disperse from hosts lacking suitable oviposition sites and to hosts that are suitable for oviposition. The result of this may be that females not ready to oviposit remain in hosts suitable for feeding and, once they are ready to oviposit, females disperse from hosts unsuitable for oviposition and remain in hosts where oviposition can be completed.

The stage of egg development may affect which females move and oviposition suitability may affect where these females remain. During the period studied, the plant structures available in the canola and forage crops were different. Forage crops were older and had thicker stems suggesting that this host was not as suitable for oviposition compared to the canola which had younger, moist, rapidly-growing plant tissues available in abundance. Thus *L. elisus* and *L. borealis* females may have moved to the canola from

the forage in search of more suitable oviposition sites. *Lygus* could still feed in all three crops, as shown by the continued residence of *Lygus* in both crops for the duration of the study. However, older forage with fewer suitable oviposition sites may have been less suitable to *L. elisus* and *L. borealis* which could have dispersed to the canola crop.

Research on the oviposition preferences of *Macrolophus caliginosus* Wagner (Ferran et al. 1996) and *L. lineolaris* (Curtis and McCoy 1964) suggests that physical stimuli are important in determining oviposition suitability in hosts. *Macrolophus caliginosus* is a mirid which utilizes its rostrum to locate and mark an oviposition site and the ovipositor is suspected to aid in evaluating host quality of plant tissue (Ferran et al. 1996). *Lygus lineolaris* shows an oviposition preference for young, moist tissue (Curtis and McCoy 1964). It is possible that physical differences in young, moist plant tissues and older plant tissues cue host suitability for oviposition in females of most *Lygus* species.

To summarize, sex ratios indicated that both *L. elisus* and *L. borealis* sex ratios are capable of deviating from 1:1 ratios and can be different from each other, particularly when compared over sampling periods. The changes to sex ratios may be the result of constant participation in dispersal events by both males and females.

Female mating status frequencies and egg development status frequencies were independent of canola crop stages. *Lygus elisus* exhibited a crop specific utilization pattern where high frequencies of females were mated and ready to oviposit in canola whereas high frequencies of females in forage crops were unmated and not ready to oviposit. In *L. borealis*, this same crop utilization pattern was even more pronounced

during the period studied. Mating status and egg development frequencies in *L. elisus* females began with high frequencies of mated females that were ready to oviposit present in the canola in late June which decreased in early-mid July then increases by early August. *Lygus borealis* mating status frequencies showed similar patterns to those of *L. elisus*, although high frequencies of females were ready to oviposit for the duration of the period studied.

Lygus elisus and *L. borealis* were found in both canola and forage crops for the duration of the study. This indicates that both crops were suitable for feeding. However, both female mating status and egg development frequencies indicated that the *L. elisus* and *L. borealis* were different in the crops compared.

5. GENERAL DISCUSSION

Lygus cause economic levels of damage in canola (*Brassica napus*) grown in the Canadian prairies (Butts and Lamb 1990; 1991; Turnock et al. 1993; Wise and Lamb 1998). *Lygus* occurring in annual stands of canola originate from movement of adults to the stand and reproduction by these adults. *Lygus elisus* and *L. borealis* collected from canola and forage plus dissections of unmated and mated *L. elisus* suggest that reproductively mature *Lygus* females move into canola.

5.1 *Lygus* Female Reproductive Processes

Lygus egg development, female mating, and oviposition are closely associated processes. There is a period of maturation which corresponds to the time required to produce eggs ready for oviposition. Female *L. elisus*, 1 day after adult eclosion, have undeveloped ovarioles lacking any visible oocytes. Previtellogenic, vitellogenic, and then chorionated oocytes are developed at approximately 4, 5, and 7 days, respectively, after adult eclosion. Unmated and mated *L. elisus* females develop previtellogenic, vitellogenic, and chorionated oocytes at the same rate, indicating that oogenesis occurs independent of mating. *Lygus elisus* females develop chorionated eggs in 7 days which approximates the 6-8 day period determined for mating receptivity in *L. hesperus* (Strong et al. 1970). This suggests that chorionated oocyte production occurs prior to mating and

that production of chorionated oocytes within ovarioles may initiate mating. Therefore, reproductively mature females are characterized morphologically by the development of chorionated oocytes within ovarioles and behaviourally by receptivity to mating. This concurs with field observations where high frequencies of female *L. elisus* and *L. borealis* contain chorionated oocytes and are mated in canola while low frequencies of female *L. elisus* and *L. borealis* contain chorionated oocytes and are mated in forage. Females without chorionated oocytes are unmated in both crops. Mating is followed by a depletion of chorionated oocytes from ovarioles (Section Three), which are oviposited into plant tissues.

Reproductive development of females was proposed to follow two patterns; (i) an initial mating occurs only after a full complement (>18 chorionated oocytes) of chorionated oocytes develops within a female's ovarioles and subsequent matings only occur after oviposition of the complete batch and a new full complement of chorionated oocytes develops within the female's ovarioles, and (ii) an initial mating occurs after development of a full complement of chorionated oocytes with subsequent mating occurring when required and further chorionated oocytes produced continuously and oviposited as they develop. The difference between the two hypotheses is the point at which subsequent mating occurs in the production of chorionated oocytes.

In hypothesis (i), all available chorionated oocytes are oviposited prior to production of more chorionated oocytes and receptivity to subsequent mating. Also, another complete batch must be developed within the female's ovarioles prior to mating. At the end of a female's reproductive life, all available chorionated oocytes are depleted

from her ovarioles and then she dies. In hypothesis (ii), the initial mating occurs after a complement of chorionated oocytes is produced but further chorionated oocyte production is not in batches. Instead, oviposited chorionated oocytes are continuously replaced by new chorionated oocytes and mating occurs when required to provide the necessary sperm fluids. In this hypothesis, the female dies with chorionated oocytes in her ovarioles. In the laboratory, one mating bout resulted in depletion of several chorionated oocytes within the ovarioles *L. elisus*. However, in the field, no reproductive *L. elisus* or *L. borealis* females contained <5 chorionated oocytes which may indicate that chorionated oocytes are continually being produced until the females die or leave the crops. This suggests that full complements of chorionated oocytes are not oviposited by females as suggested by hypothesis (i). Instead, chorionated oocytes are produced continually after the initial mating and females never deplete chorionated oocytes as suggested in hypothesis (ii).

5.2 Female Reproductive Maturity and its Association to *Lygus* Movement

Lygus overwinter in litter or plant cover and in the spring, overwintered adults move to and feed on early-growing plants (Craig 1983). Perennials like forage crops not only provide overwintering sites but also early growth (mid-May to mid-June) suitable for *Lygus* feeding. In contrast, commercially grown canola is a suitable host for *Lygus* feeding but, because it is an annual, *Lygus* that have not developed from eggs oviposited within that host, can only appear there through movement from another host. Also, the first *Lygus* nymphs were not present in the canola until July and any *Lygus* adults

collected in the canola had to originate from another host. Therefore, sampling from the rosette to flower canola growth periods, only immigrant adults were examined. Of these females, high numbers of *L. elisus* and *L. borealis* have partly deflated seminal depositories and contain chorionated oocytes. This suggests that *Lygus* females moved when they are ready to oviposit and after they have mated.

Insect movement is generally defined as dispersal or migration and one of the defining characteristics used to distinguish between these two definitions is reproductive status. Kennedy (1961), defined migration as movement involving the inhibition of reproduction, including adults that were non- or pre-reproductive. Johnson (1966) defined migration as including pre- or non-reproductive adults and used the term oogenesis-flight syndrome to describe migration by young adults in which oogenesis is inhibited. Dingle (1972) said that migrating individuals should move prior to reproductive maturity to habitats suiting development of offspring. If we examine *Lygus* movement as exemplified by *L. elisus* and *L. borealis*, movement into canola from June to early August, *Lygus* disperse to canola. During the period studied, migration, as defined by Kennedy (1961), is not occurring, and the oogenesis-flight syndrome (Johnson 1966) does not apply to *Lygus*. Instead, *Lygus* appear to disperse when adults have mated already possess chorionated oocytes.

5.3 *Lygus* Reproduction in Relation to Canola Crop Stage

Mating status and egg development frequencies were not related to different canola crop stages or staggered seeding dates of canola. In 1994 and 1995, high

frequencies of *L. elisus* and *L. borealis* females collected from different (11 May and 14 June) seedings of canola were mated, as indicated by the size of the seminal depository, and contained chorionated oocytes. This suggests that canola was utilized for oviposition by *L. elisus* and *L. borealis*.

Lygus likely follow a movement pattern where reproductively mature females move into available canola stands. In southern Alberta, high frequencies of *L. elisus* and *L. borealis* females contain chorionated oocytes beginning in June then this decreases from late-June to early August followed by an increase in late August. From June to early August, high frequencies of these same females are mated over the comparable periods. Results from dissected *L. elisus* suggest that production of chorionated oocytes within ovarioles coincides with mating receptivity (Section 3).

5.4 *Lygus* Species Differences

Lygus elisus and *L. borealis* generally adhere to similar mating and egg development patterns however the two species are different. Comparison of *L. elisus* and *L. borealis* mating status frequencies indicate that higher frequencies of *L. borealis* females than *L. elisus* females were categorized as mated in the canola. Generally similar frequencies of *L. borealis* and *L. elisus* females were categorized as mated in the forage crops. Relatively higher frequencies of female *L. borealis* contained chorionated oocytes than *L. elisus* in the canola. Generally, similar low frequencies of *L. borealis* and *L. elisus* females contained chorionated oocytes in the forage crops. This was related to the finding that the majority of females in the forage were reproductively young, as indicated by the

absence of chorionated oocytes ovarioles associated with adult female *Lygus* ≤7 days old (Section 3). In the forage crops, *L. elisus* and *L. borealis* are more similar but there were fewer reproductively mature females of both species in this crop. Therefore, there is less variation possible in mating and egg development status compared to females collected in canola.

The mating status and egg development results show that *L. elisus* and *L. borealis* are not identical in their development. However, during the period studied, high numbers of females of both species collected from the canola were ready to oviposit and mated. In the forage, low numbers of female *L. elisus* and *L. borealis* were ready to oviposit and mated. These results do suggest that *L. elisus* and *L. borealis* reproductive status, in terms of practical management and control in canola and forage crops, could be dealt with as a "*Lygus* complex". Fye (1982) groups several *Lygus* species together as a complex because each species inflicts the same type of injury and they coexist within one field. In addition to coexistence and damage inflicted, this study indicates that female reproductive status also is similar between *L. elisus* and *L. borealis*. This suggests that in southern Alberta, in terms of management and control, these two dominant species of *Lygus* (Schwartz and Footitt 1992) could be considered as a complex.

5.5 Sex Ratios

Comparison of *L. elisus* and *L. borealis* sex ratios did not show bias towards either females or males in either canola or forage crops. Sex ratios did not deviate from 1:1 in 1994 but deviations were common in 1995 with both male and female bias occurring.

Overall, no pattern is evident in *L. elisus* and *L. borealis* sex ratios although, sex ratios did consistently change between sampling periods compared. The 1:1 sex ratio observed in laboratory reared *L. lineolaris* (Fleischer and Gaylor 1988) may be present in both *L. elisus* and *L. borealis* but the variable sex ratio results do not indicate any predictable relationship between sex ratios and canola crop stage or any temporal period examined in this study.

5.6 Conclusions

Dissections of colony reared *L. elisus* indicate that egg development is independent of mating but mating does not occur until there is a large complement of chorionated oocytes within a female's ovarioles. In the field, females which possess a large complement of chorionated oocytes are usually mated. Females lay chorionated oocytes continuously once mated. The longevity of reproductive females and possibility of multiple mating needs to be further investigated in order to more accurately estimate age of field collected *Lygus*.

Sex ratios fluctuated from sample to sample but there was no consistent pattern. Constant movement by both sexes may result in the apparent temporal change in sex ratio. However, in the large population, the ratio is likely 1:1.

Female reproductive status is associated with *Lygus* movement. Higher frequencies of female *L. elisus* and *L. borealis* contain chorionated oocytes and are mated in canola stands (rosette to flower stages) from June to early August compared to those in forage. This suggests that *L. elisus* and *L. borealis* (1) are older in the canola than in the

forage, (2) utilize canola and forage crops differently based on the completion of reproductive, as opposed to strictly feeding, activities, (3) reproductive status is not synchronized with a particular canola crop stage, and (4) exhibit a movement pattern in which individuals participating in movement are reproductively mature. Based on this study, *L. elisus* and *L. borealis* movement is a dispersal event whereby reproductively mature females move from one host to another.

6. SUMMARY AND CONCLUSIONS

Oogenesis occurs independent of mating in *L. elisus* females. The ovarioles which house developing oocytes are undeveloped in newly eclosed females. Both unmated and mated females produce previtellogenic, vitellogenic, then chorionated oocytes within ovarioles at 4, 5, then 7 days, respectively. Production of chorionated oocytes is hypothesized to proceed mating receptivity. Mating results in a decrease in the number of chorionated oocytes from within ovarioles, although the previtellogenic region of the ovarioles remains visibly intact. The reduction is likely due to continuous oviposition by mated females.

Lygus female reproduction is associated with movement into economically important crops such as canola. Both males and females disperse into canola at a similar time because no pattern in sex ratios was evident. *Lygus elisus* and *L. borealis* sex ratios were sometimes either male or female biased and fluctuated with no apparent pattern. Higher frequencies of female *L. elisus* and *L. borealis* contain chorionated oocytes and are mated in canola stands (rosette to flower stages) from June to early August compared to those in forage. This suggests that most *L. elisus* and *L. borealis* are older in the canola than in the forage. *Lygus elisus* and *L borealis* utilize canola and forage crops differently based on the completion of reproductive, as opposed to strictly feeding, activities. High frequencies of mated, ready to oviposit *L. elisus* females were present in

the canola in late June which decreased in early-mid July then increased by early August. High frequencies of *L. borealis* females were mated and contained chorionated oocytes for the duration of the study period. *Lygus elisus* and *L. borealis* move when females are reproductively mature. The finding that high frequencies of mated females that were present in the canola compared to high frequencies of unmated, reproductively immature females in the forage during the same period, suggests that *L. elisus* females in forage are younger, that they mature reproductively in forages then, once mated and ready to oviposit, are found in canola where they oviposit. Based on this study, *L. elisus* and *L. borealis* movement is a dispersal event whereby reproductively mature females move from one host to another.

7. CONTRIBUTIONS TO KNOWLEDGE

By examining the reproductive biology of *L. elisus* females using unmated and mated individuals, this study has shown that egg development occurs independent of mating. Females are likely receptive to mating once chorionated oocytes are developed within ovarioles. Mating results in expansion of the seminal depository in females. With time, the seminal depository in mated females gradually decreases in size and the number of chorionated oocytes within ovarioles decreases as oocytes are oviposited.

This study demonstrated that *L. elisus* and *L. borealis* reproduction is associated with movement. In the forage, unmated *L. elisus* and *L. borealis* females which were not ready to oviposit chorionated oocytes were present but mated and ready to oviposit chorionated oocytes in the canola during the same sampling period. This suggests that females in the forage are younger than those in the canola. Females likely feed and mature reproductively in the forage then move to canola to mate or to oviposit. Finally, females are capable of discerning between hosts and move accordingly to oviposit on suitable hosts. *Lygus* oviposition preferences should be examined to determine plant characteristics that deter oviposition. Physical qualities of the plant, e.g., moisture levels, trichome density, or age of plant structures may affect *Lygus* oviposition preferences. Plant characteristics deterring oviposition might be used by plant breeders to provide plant protection through breeding programs.

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9. APPENDIX I

Figure 24. Mean abundance of *Lygus* species from 100 sweeps performed in crops in 1994. Sweep-net collections were performed during sampling periods defined as the days elapsed when the early and late seeded stands of canola were at the early rosette (172-179), bud (180-186), flower (187-191), late rosette (192-195), bud (196-205), and flower (206-210) crop stages. A. *Lygus elisus* (Van Duzee) collected in canola; B. *Lygus elisus* (Van Duzee) collected in alfalfa; C. *Lygus borealis* (Kelton) collected in canola; D. *Lygus borealis* (Kelton) collected in alfalfa.

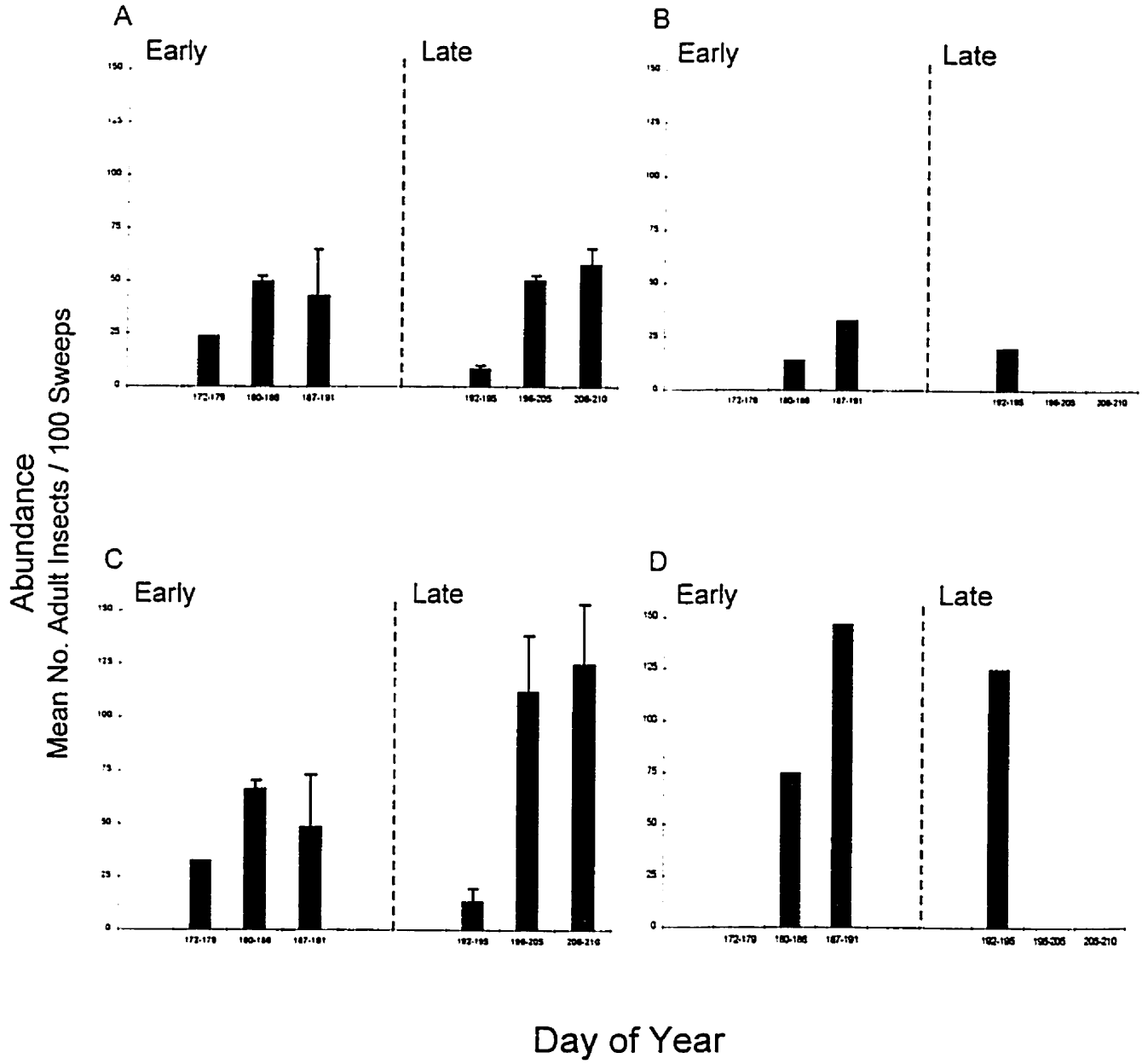
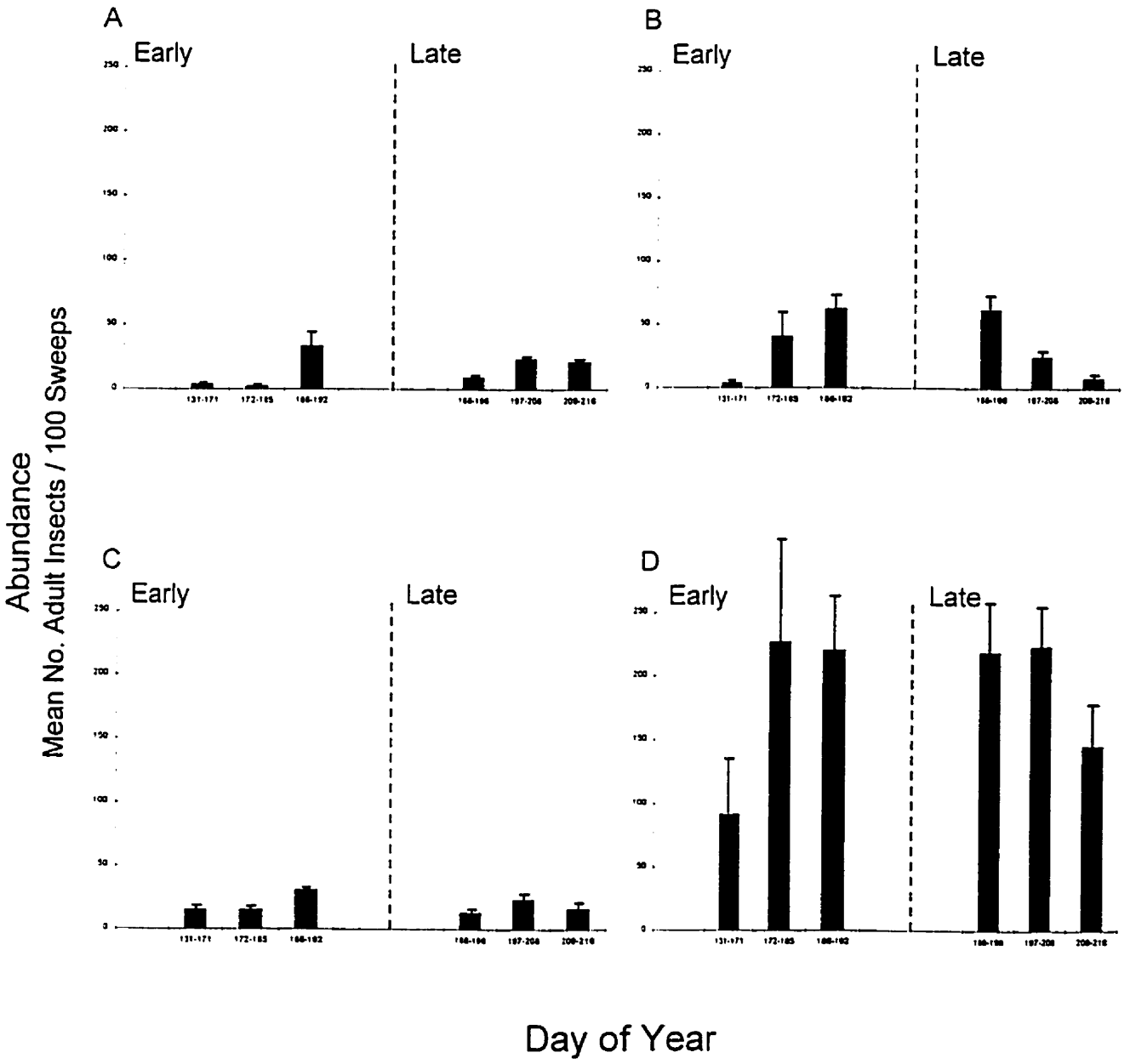

A
Early
Late
B
Early
Late
C
Early
Late
D
Early
Late
Abundance
Mean No. Adult Insects / 100 Sweeps
Day of Year

Figure 25. Mean abundance of *Lygus* species from 100 sweeps performed in crops in 1995. Sweep-net collections were performed during sampling periods defined as the days elapsed when the early and late seeded stands of canola were at the early rosette (131-171), bud (172-185), flower (186-192), late rosette (188-196), bud (197-208), and flower (209-216) crop stages. A. *Lygus elisus* (Van Duzee) collected in canola; B. *Lygus elisus* (Van Duzee) collected in alfalfa; C. *Lygus borealis* (Kelton) collected in canola; D. *Lygus borealis* (Kelton) collected in alfalfa.


A
Early
Late
B
Early
Late
C
Early
Late
D
Early
Late
Abundance
Mean No. Adult Insects / 100 Sweeps
Day of Year

10. APPENDIX 2

Table 23. Mean and range number of chorionated and vitellogenic oocytes in *Lygus elisus* and *L. borealis* females collected in canola (*Brassica napus* L. cv. Westar) and sainfoin (*Onobrychis viciaefolia* Scop. cv. Nova) in 1995.

Lygus species	Host crop	Size of seminal depository	Mean number of chorionated oocytes (±SE)	Range number of chorionated oocytes	Mean number of vitellogenic oocytes (±SE)	Range number of vitellogenic oocytes	Sample size (N)
Lygus elisus	Canola	uninflated	0.0 (±0.04)	0-6	0.1 (±0.08)	0-10	143
		inflated	13.2 (±0.50)	0-38	4.8 (±0.33)	0-30	199
		partly deflated	15.1 (±0.33)	0-50	9.7 (±0.27)	0-34	558
		deflated	3.9 (±0.97)	0-28	4.4 (±0.92)	0-36	54
	Sainfoin	uninflated	0.01 (±0.04)	0-6	0.1 (±0.04)	0-6	174
		inflated	12.3 (±1.88)	0-25	4.1 (±0.82)	0-10	18
		partly deflated	14.6 (±1.06)	0-35	5.4 (±0.63)	0-22	55
		deflated	4.6 (±3.27)	0-46	3.1 (±1.19)	0-14	14
Lygus borealis	Canola	uninflated	0.4 (±0.26)	0-30	0.2 (±0.09)	0-9	144
		inflated	15.0 (±0.29)	0-35	3.5 (±0.14)	0-20	539
		partly deflated	17.0 (±0.27)	0-56	5.4 (±0.15)	0-26	769
		deflated	11.4 (±1.82)	0-33	4.5 (±0.69)	0-14	34
	Sainfoin	uninflated	0.01 (±0.01)	0-7	0.1 (±0.04)	0-13	534
		inflated	15.3 (±0.58)	0-35	2.7 (±0.18)	0-12	132
		partly deflated	15.4 (±0.58)	0-53	4.4 (±0.40)	0-25	160
		deflated	2.4 (±1.19)	0-21	2.1 (±0.73)	0-14	21